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ALYTES

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Editorial

Alain DUBOIS

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Following the workshop on "Declining amphibian populations – a global phenomenon?" held in Irvine (California, USA) on 19-20 February 1990 (see WAKE et al., 1991) and the subsequent foundation of the Declining Amphibian Population Task Force (DAPTF), the study of amphibian population declines and of their causes has become a major research field (see review in ALFORD & RICHARDS, 1999). The scientific literature dealing with these questions has been dispersed in various periodicals. The quarterly journal *Froglog*, published by DAPTF, regularly provides reviews and bibliographic lists regarding this field of research. Until now, the journal *Alytes* has seldom been used as an outlet for the publication of such reports. This is unfortunate, as *Alytes* is the only journal in the world entirely dedicated to the publication of scientific works dealing with amphibians, and as the International Society for the Study and Conservation of Amphibians (ISSCA), the non-profit association that publishes this journal, has among its statutory aims "to contribute, on a world scale (...) to the conservation of Amphibians and to that of their environment" (ANONYMOUS, 1994: 62). In order to call attention to the possibility of publishing papers dealing with amphibian declining populations, and, more generally, with all problems related with the conservation biology of amphibians, the ISSCA Board has decided to create a third position of Editor for the journal, that of Conservation Editor. Stephen J. Richards (Adelaide, Australia) has agreed to take on this responsibility. All amphibian biologists working on questions related to the conservation of amphibians, to declining populations, their causes and possible remedies, are warmly invited to submit their manuscripts to Steve. From now on, manuscripts intended for *Alytes* can be submitted to three different editors, who will care for their submission to referees, for correspondence with the authors and for the final decision regarding them:

– Alain Dubois (Laboratoire des Reptiles et Amphibiens, Muséum National d'Histoire Naturelle, 25 rue Cuvier, 75005 Paris, France; <dubois@mnhn.fr>), for any paper dealing with amphibian morphology, anatomy, systematics, biogeography, evolution, genetics, anomalies or developmental biology;

– Thierry Lodé (Laboratoire d'Ecologie animale, Université d'Angers, 2 boulevard Lavoisier, 49045 Angers Cedex, France; <thierry.lode@univ-angers.fr>) for any paper dealing with amphibian population genetics, ecology, ethology or life history;

– Stephen J. Richards (Vertebrates Department, South Australian Museum, North Terrace, Adelaide, S.A. 5000, Australia; <Richards.Steve@saugov.sa.gov.au>) for any paper dealing with declining amphibian populations, amphibian pathology, and more generally with all matters related to amphibian conservation biology.

Another recent decision of the ISSCA Board has been to act for more regularity in the publication of *Alytes*. From now on, and for an undetermined number of years, the journal will be published as two double (or one single and one triple) issues per year, at fixed dates, in May and November. This schedule will be maintained irrespective of the number of papers and pages accepted for publication at these dates. The result will be that some issues (like this one) will be somewhat thin, while others (like next one) will be much thicker: despite this, all effort will be made to provide subscribers and readers with our usual number of 200 pages or more per year. Hopefully, this change in the publication schedule of the journal will be appreciated by our subscribers: from now on, it will be possible to foresee the dates of publication of the journal, instead of receiving it suddenly at unexpected dates. Our readers are welcome to let us know their feelings about these new changes in our journal, just before it reaches the age of 20!

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Alytes, 2001, **19** (1): 2-4.

A replacement name for *Rana (Paa) rara* Dubois & Matsui, 1983 (Amphibia, Anura, Ranidae, Raninae)

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A replacement name is proposed for the frog species *Rana (Paa) rara* Dubois & Matsui, 1983 from north-western Nepal, as the latter name proves to be a junior primary homonym of *Rana danubina rara* E. Fraas, 1903, a name given to a fossil frog species from the Miocene of Germany. A lectotype is designated here for the latter taxon.

DUBOIS & MATSUI (1983: 895) described a new frog species from Rara lake in north-western Nepal under the name *Rana (Paa) rara*. DUBOIS (1992: 320) raised the subgenus *Paa* Dubois, 1976 to the rank of genus, with three subgenera, and recognized this species as *Paa (Paa) rara* (Dubois & Matsui, 1983).

This name, however, cannot be conserved for this species, as it is a junior primary homonym in the genus *Rana*, being preoccupied by the name *Rana danubina* var. *rara* E. Fraas, 1903. The history of the latter name, however, is a little complicated, and deserves some discussion.

In a paper dealing with the Miocene fossil fauna of Steinheim am Albruch (48°41'N, 10°03'E; Baden-Württemberg, Germany), Oscar FRAAS (1870: 291) mentioned once the new name *Rana rara*, but without providing any information about this species: as rightly remarked by SANCHIZ (1998: 142), this name is therefore a nomen nudum, without nomenclatural status. According to this later author, this name was based on a tibio-fibula, still kept in the collection of the Staatliches Museum für Naturkunde of Stuttgart under number SMNS 80207, and which "probably belongs to a small mammal (R. Böttcher, in litt., 1995)".

More than thirty years later, E. FRAAS (1903) described in detail a complete articulated fossil frog skeleton from the Miocene of Steinheim, for which, instead of coining a new name, he used the name *rara* proposed by his father, but as a subspecific name, using the combination *Rana danubina* var. *rara*. SANCHIZ (1998: 130) stated that, in this combination, the specific epithet *danubina* was an "unwarranted spelling change" for the specific name *Rana danubiana*, proposed by MEYER (1858: 203), but this does not tell us whether this epithet has, or not, a status in nomenclature (see e.g. DUBOIS, 1987, 2000). Actually, the spelling *danubina* was

Source : MNHN, Paris

introduced by MEYER (1860: 142), who used it consistently in his text and figure legend, so that we regard it as an unjustified emendation of *danubiana*, therefore a name having an independent status in nomenclature and its own author and date (i. e., MEYER, 1860).

As for the epithet *rara*, E. FRAAS (1903: 105-106) borrowed it to his father's work (where it applied to an isolated tibio-fibula), but used it to name the new complete skeleton collected by A. Pharion in 1902, and also applied it with some doubts to a third specimen from Steinheim, a radio-ulna found by C. Joos. He provided (E. FRAAS, 1903: 107-108) a very detailed description of the complete skeleton, with measurements. Earlier in the paper (E. FRAAS, 1903: 105), he had also given a photograph of this fossil that clearly shows a frog. As rightly commented by SANCHIZ (1998: 130), by providing a description, E. FRAAS (1903) gave for the first time a nomenclatural status to the epithet *rara*, as *Rana danubina rara* E. Fraas, 1903.

Because he assumed that only one specimen was involved, SANCHIZ (1998: 130) stated that the "holotype" of this nominal species was the complete articulated skeleton found by A. Pharion in Steinheim, still kept in Stuttgart under number SMNS 11354, and that should be referred to the "*Rana (ridibunda)* group" (SANCHIZ, 1998: 130), i.e. to the subgenus *Rana (Pelophylax)* (DUBOIS & OHLER, 1995). However, E. FRAAS (1903) never used the terms "holotype" or "type" for this skeleton, and his use of the name *Rana rara* proposed by his father suggests that the name *Rana danubina rara* must be considered based on at least two syntypes, the original isolated tibio-fibula and the new articulated skeleton; whether or not it was also based on the third specimen, the isolated radio-ulna, is more open to discussion, but the inclusion of the original bone (implied by the use of the name *rara*) suggests that it was also the case for this second isolated bone. Because both isolated bones are of doubtful taxonomic allocation (and possibly not frogs), it is important for the future allocation of the name *rara* to designate a lectotype among these two (or three) syntypes. To stabilize definitely the status of this name, we hereby designate the articulated skeleton, SMNS 11354, as lectotype of *Rana danubina rara* E. Fraas, 1903. This name was considered by SANCHIZ (1998: 130) as a junior subjective synonym of *Rana danubiana* Meyer, 1858, a name based on an incomplete articulated frog skeleton from the Miocene of Günzburg (48°27'N, 10°16'E; Bayern, Germany), that was "presumably destroyed in 1944" (SANCHIZ, 1998: 130). Stabilization of the nomenclatural status of the latter name (considered as a "nomen dubium" by SANCHIZ, 1998) would require the discovery and designation as neotype of another specimen from Günzburg and from the same stratigraphic level as the lost holotype, which is not the case of the lectotype of *Rana danubina rara* (see SCHLEICH, 1981).

To the best of our knowledge, after E. FRAAS's (1903) paper, his name *rara* was mentioned only twice in the literature: by KUHN (1938: 16), as *Rana danubiana* var. *rara*, and by SANCHIZ (1998: 130), as a junior subjective synonym of *Rana danubiana* Meyer, 1858. A neotype designation would stabilize definitively this synonymy. Nevertheless, even if the name *Rana danubina rara* disappeared definitely from scientific literature as a permanent junior synonym, this would have no bearing on the nomenclatural *availability* of this name (for more details, see DUBOIS, 2000), and the epithet *rara* E. Fraas, 1903 will always remain available and will preoccupy the use of the same epithet in the nominal genus *Rana*.

As a matter of fact, according to Articles 57 and 60 of the *Code* (ANONYMOUS, 1999), a junior primary homonym "is permanently invalid" and must be replaced. As the name *Rana*

Source : MNHN, Paris

(Paa) rara Dubois & Matsui, 1983 is not known to have a synonym, we have to provide a nomen novum (new replacement name) for the *Paa* species. Therefore we propose the nomen novum *Paa (Paa) rarica* for the species described by Dubois & Matsui (1983). The adjective *rarica* means "from Rara", "living in Rara", and refers to the type-locality of the species, Rara lake (Rara Daha; 29°31'N, 82°05'E; 2990 m; Jumla Province; Nepal), which until now remains the only known locality of occurrence of the species.

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Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 2. Morphological and molecular variation in frogs from the Greater Sunda Islands (Sumatra, Java, Borneo) with the definition of two species

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Frogs of the species *Fejervarya limnocharis* and related species are among the most common in Southeast Asia. We studied 52 individuals from eight populations of the Great Sunda Islands by means of allozyme electrophoresis, mtDNA sequencing and morphometry. Patterns of variation of all characters among populations were congruent in separating one Javanese population from all other populations (Java, Sumatra, Borneo) as a distinct species. The frequencies of four distinct mid-dorsal stripe showed no distinct geographic pattern. Morphometric analysis unambiguously permits assignment of the name *Rana limnocharis* Gravenhorst, 1829 to the widespread form that occurs in Java, Sumatra and Borneo. The two taxa recognised in this study occur in sympatry in Java. As the taxon known only from Java lacks a name, we describe and name it.

ABBREVIATIONS

FMNH	Field Museum of Natural History, Chicago, USA.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
RMNH	Nationaal Natuurhistorisch Museum, Leiden, Netherlands.
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

Source : MNHN, Paris

Introduction

Description of existing biodiversity is one of the main goals of conservation biology. Especially in the tropics very little is known about the real number of species and our knowledge on intraspecific variability of tropical animal and plant species is even lower. The Amphibia of most parts of the Oriental faunal region have been poorly studied until now (Inger, 1999). This holds especially for the Greater Sunda Islands, although two reviews of its batrachofauna were recently published (Manthey & Grossmann, 1997; Inger & Stuebing, 1997). Within the last decades, many new species have been described from these islands based on morphological traits (e.g., Inger, 1989; Inger & Gritis, 1983; Inger & Stuebing, 1991, 1997). However, the few biochemical studies on Southeast Asian anurans have made apparent that a great amount of cryptic variation is present within species (e.g., Inger et al., 1974; Donnellan et al., 1989; Kosuch et al., 1997; Toda et al., 1998*a*).

The ranid genus *Fejervarya* Bolkay, 1915 is distributed throughout Southeast Asia (Dubois & Ohler, 2000). These species show substantial morphological and colour variation over their distribution range. In Nepal, studies of mating calls showed the co-existence of four species (Dubois, 1975). In their study on genetic divergence among Southeast Asian *Rana limnocharis,* Toda et al. (1997, 1998*a-b*) discovered genetic divergence and sympatric cryptic species in this group without morphological differentiation.

The present study focuses on the variation within frogs known as *Fejervarya limnocharis* (Gravenhorst, 1829) in the Greater Sunda Islands, a group of frogs that are known to be abundant in areas of intensive human activities (Inger, 1966; Inger & Stuebing, 1989; Manthey & Grossmann, 1997). To describe the pattern of variation in this common frog group we compared the within- and between-island variability of molecular and morphological traits.

The nomenclatural situation in this group of frogs was presented in detail in part 1 of this series of papers (Dubois & Ohler, 2000). Generic classification follows Dubois (1992), slightly modified by phylogenetic data of DNA analysis (Marmayou et al., 2000). In order to formalise the systematic position of the different forms of *Fejervarya* found in our genetic analysis, we linked molecular data to morphometric data. This allows us to cross-reference old names based on museum specimens with results of modern molecular population studies.

Material and methods

Frogs were collected from six natural populations or bought from local fish markets of Java (J), Sumatra (S) and Kalimantan (K), the latter being the Indonesian part of Borneo (fig. 1): J1 (4 specimens, FMNH 256721-256724), swampy meadow along the road between Bogor and Parung; J2 (11 specimens, FMNH 256725-256733, MNHN 1997.4916, ZMFK 68867), paddy field at Chianjur; K1 (2 specimens, FMNH 256734-256735), fish market at Pontianak; K3 (12 specimens, FMNH 256736-256747), paddy field at the village Desa Lape; S1 (13 specimens, FMNH 256749-256761), fish market at Medan; S2 (2 specimens, FMNH 256762-256763), paddy field and small brook at village Sidikalang; S5 (5 specimens, FMNH 256764-

Source : MNHN, Paris

Fig. 1. – Sample localities of *Fejervarya* on the Great Sunda Islands, Indonesia (* refers to the sample locality 3/4 of TODA et al., 1998*a*).

256768), frogs collected by inhabitants at a small village about 10 km SE Tapaktuan; S6 (3 specimens, FMNH 256769-256771), frogs collected by inhabitants of the village Desa Seleukat near Tapaktuan. In the molecular analyses we used the ranids *Fejervarya cancrivora* (Gravenhorst, 1829) (Kalimantan, Borneo), *Rana temporaria* Linnaeus, 1758 (Germany) and *Rana catesbeiana* Shaw, 1802 (from a frog farm at Java) as outgroups.

A specimen from the collection of Heinrich Kuhl from Java (RMNH 4287), designated as neotype of *Rana limnocharis* Gravenhorst, 1829 by DUBOIS & OHLER (2000), was included in a discriminant analysis for nomenclatural decisions.

Sex of all specimens was determined either by presence of secondary sexual characters or by observation of gonads through small lateral or ventral incision on the frogs (most of the frogs were ventrally opened because of tissue dissection in the field).

ALLOZYME ELECTROPHORESIS

Pieces of fresh muscle and liver were dissected and stored in liquid nitrogen. Frogs were preserved for determination and morphometry in 70 % alcohol after pre-fixation in 10 % formaldehyde.

Source : MNHN, Paris

Allozyme electrophoresis was carried out on muscle and liver homogenates on cellulose acetate gels (RICHARDSON et al., 1986). Twelve enzyme systems providing information on 15 presumptive gene loci were stained according to HEBERT & BEATON (1986). Gels were run in three different buffer systems: tris-glycine, pH 8.5 [*acon-1* and *-2* (E.C. 4.1.1.3), *fum* (E.C. 4.2.1.2), *aat-1* and *-2* (E.C. 2.6.1.1), *mdh* (E.C. 1.1.1.37), $pep_{Gly\text{-}Leu}$ (E.C. 3.4.11), *pgm* (E.C. 5.4.2.2) and *tpi* (E.C. 5.3.1.1)], tris-citrate, pH 7.0 [*idh-1* and *-2* (E.C. 1.1.1.42), *me* (E.C. 1.1.1.40) and *mpi* (E.C. 5.3.1.8)] and phosphate, pH 8.0 [*ldh* (E.C. 1.1.1.27) and *pk* (E.C. 2.7.1.40)]. Average expected heterozygosity (H_e) and mean number of polymorphic loci (P) were calculated as population characteristics using the computer program G-STAT (SIGISMUND, 1993). NEI's (1972) standard genetic distance estimates and UPGMA cluster analysis were calculated using the program NTSYS (ROHLF, 1990).

DNA-SEQUENCING

DNA was extracted from frozen muscle tissue using the standard phenol-chloroform protocol of SAMBROOK et al. (1989). Double-stranded PCR amplification was performed in 50 µl reactions containing 1 unit of Taq polymerase, 5 µl of 10 × reaction buffer (Boehringer), 250 µmol each of dGTP, dATP, dTTP and dCTP, 20 pmol each of light- and heavy-strand primers and 1 µl of mtDNA extract. The primers 16Sa-L and 16Sb-H (KOCHER et al., 1989) amplified a double-stranded DNA segment of 560 bp of the mitochondrial 16S ribosomal RNA gene. Thermal cycling was carried out in a programmable heating block (Perkin Elmer Gene Amp PCR System 9600) for 35 cycles (initial denaturation step of 90 s at 94°C, denaturation for 45 s at 94°C, primer annealing for 45 s at 55°C and extension for 90 s at 72°C).

PCR products were purified with a PCR purification kit (QuiaQuickspin) and directly sequenced with a sequenase kit (Amersham) using only primer 16Sa-L. The products of the sequencing reaction were resolved by the automatic sequencer 377 of Applied Biosystems.

After sequence alignment with CLUSTAL-W (HIGGINS & SHARP, 1993), the alignment was adjusted manually. The aligned 390 bp sequence corresponds to nucleotides 4039-4429 in the *Xenopus laevis* mitochondrial genome (ROE et al., 1985). Phylogenetic relationships were determined using maximum parsimony (PAUP, version 3.1.1; SWOFFORD, 1993) and maximum likelihood approaches (PHYLIP, version 3.5c; FELSENSTEIN, 1993). For maximum parsimony analysis, 1000 bootstrap replicates were run to test for confidence in the topology of the phylogenetic trees (FELSENSTEIN, 1985).

Sequences have the GenBank accession numbers AF346810-AF346811, and the EMBL accession numbers AJ292014-AJ292023.

MORPHOMETRY

Twenty-seven measurements of 39 adult specimens were taken with a slide caliper to 0.1 mm precision or for measurements smaller than 5 mm with an ocular micrometer to the nearest 0.01 mm (app. 1). To control for isometry, all measurements were divided by snout-vent length (SVL), expressed as per thousands of SVL, or transformed into the Neperian logarithm. Male and female specimens were grouped after their homogeneity was established

Source : MNHN, Paris

(OHLER, 1996). For morphometrical analyses we used SPSS statistical programs for personal computers (NORUSIS, 1992)

Morphological analysis should test if genetically close populations from different islands are also morphologically homogenous and, conversely, if the two genetically differentiated species can be distinguished by their morphology. Non-parametric Kruskal Wallis test was performed to measure morphological variation in *Fejervarya* specimens of different islands. Differentiation between genetically distinct samples was tested using non-parametric Mann-Whitney *U* test.

Discriminant analysis

Groups obtained by the molecular analyses were subjected to a discriminant analysis (NORUSIS, 1992) The measurement data for the female neotype of *Rana limnocharis* were incorporated into the analysis after the production of the original discriminant function model based on all other data, following examples of nomenclatural clarification using this approach (HEYER, 1994; OHLER, 1999; OHLER & DUBOIS, 1999).

Colour patterns

Frogs of the genus *Fejervarya* are known to frequently have mid-dorsal stripes, which are an interesting character for evolutionary biology studies (see e.g MILSTEAD et al., 1974; DUBOIS, 1980). Heritability studies by MORIWAKI (1953) and MOHANTY & DUTTA (1999) suggested that presence or absence of a dorsal line in *Fejervarya* is coded by two alleles of a single locus. The allele for the striped phenotype appears to be dominant over that for the unstriped one. However, MORIWAKI (1953) and others (e.g., SHIBATA, 1988) only discriminated between two phenotypes (striped and unstriped). DUBOIS (1977) and MOHANTY & DUTTA (1999) distinguished between three phenotypes, a pattern showing no line at all, a pattern showing a fine line and a third pattern showing a wide stripe The patterns are not distributed equally in the four different species of *Fejervarya* from Nepal which can be distinguished by their mating calls, whereas *F teraiensis* (Dubois, 1984) and *F pierrei* (Dubois, 1975) show all three different patterns, *F syhadrensis* (Annandale, 1919) does not show the wide stripe phenotype, and all *F nepalensis* (Dubois, 1975) specimens have mid-dorsal stripes (DUBOIS, 1977)

Four mid-dorsal patterns can be recognised in the *Fejervarya* specimens that we studied (fig 2): (1) no mid-dorsal line or stripe, (2) a fine clear mid-dorsal line alone present, (3) a wide mid-dorsal stripe alone present, (4) both a fine line and a wide stripe present, superimposed. Presence and absence of both kinds of lines as well as frequency of combination of the two lines and their distribution among populations were noted, and their pattern of variation was studied using Kruskal-Wallis test.

MUSEUM PARIS

Source : MNHN, Paris

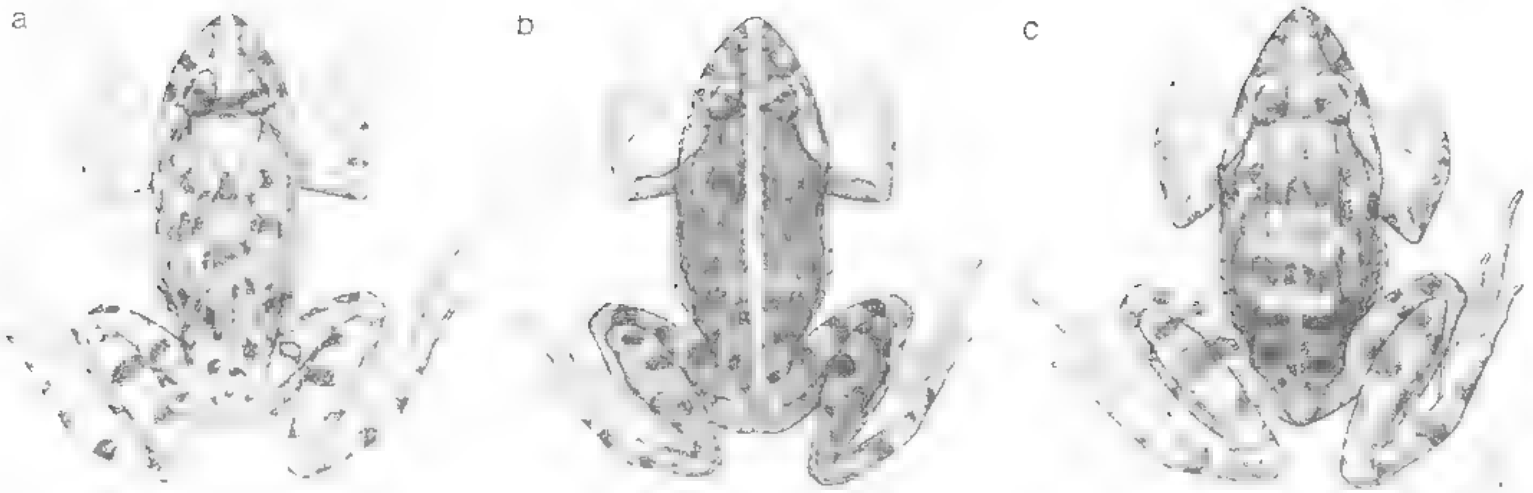

Fig. 2. — (a) Holotype of *Fejervarya iskandari* MNHN 1997 4916, from Chianjur, Java, phenotype no line/no stripe, 16S haplotype J2-C, (b) *Fejervarya limnocharis* from Desa Lape, Borneo, phenotype line/stripe, 16S haplotype K3-A, (c) *Fejervarya limnocharis* from Tapaktuan 2, Sumatra, phenotype line/no stripe, 16S haplotype S5-A. Drawings by Käthe Rehbinder, Mainz.

Source : MNHN, Paris

RESULTS

ALLOZYME VARIATION

Of the 15 allozyme loci studied, five were monomorphic (*fum*, *idh-1*, *idh-2*, *me*, *pk*) within and between the *Fejervarya* samples. *Acon-1*, *acon-2* and *ldh* were monomorphic within populations, but exhibited a fixed allelic difference in population J2 relative to all other populations (app. 2). Between populations J1 and J2 further allelic differences appeared to be fixed at the loci *aat-2*, *mpi* and *pep*. Thus, these two geographically closely related populations did not share alleles at six out of 15 loci.

Intra-populational genetic variability (H_e) was lowest in the Sumatran samples with the exception of sample S1 from the Medan fish market. This was the only sample that showed significant genotype deviations from Hardy-Weinberg expectation at two loci (*mpi* and *pep*; $P < 0.05$) due to a lack of heterozygous specimens, indicating a mix-up of different populations. Sample S5 was completely monomorphic. Three to six loci were polymorphic in the Javanese and Borneo samples, even though sample sizes were in some cases lower than for S5.

NEI's (1972) standard genetic distance between populations ranged from 0.004 between S1 and S2 and 0.337 between J2 and S5 (tab. 1). Population J2 was the genetically most distinct. It was separated even from the geographically close population J1 by a relatively high genetic distance estimate of 0.316. The Borneo and Sumatra populations formed distinct clusters in the UPGMA phenogram (fig. 3).

MTDNA SEQUENCE DIVERGENCE

We sequenced 390 bp of the mitochondrial 16S rRNA gene from 52 individuals of *Fejervarya* and from the three outgroup species. One hundred twenty seven bp positions were variable. Samples of *Fejervarya* comprised nine different haplotypes (tab. 2) with 60 sites being variable among them. Fifty-two of these variable sites were parsimonious informative, 49 of which supported the monophyly of either of the two main haplotype lineages.

The average substitution rate between the haplotypes of population J2 and the remaining populations from Java, Sumatra and Borneo was 0.135. This is only about 0.02 less than between either of the two *Fejervarya* forms and *F. cancrivora*, thus suggesting the differentiation of J2 from the other *Fejervarya limnocharis* populations as distinct species.

The maximum parsimony and maximum likelihood trees produced exactly the same topology with two rather homogeneous but well differentiated groups of *Fejervarya* mitochondrial 16S haplotypes (tab. 3). Bootstrap support in the maximum parsimony tree was 100 % for both clades (fig. 4) which we subsequently name J1 and J2. No further significant topology was found within the two clades.

Source : MNHN, Paris

Table 1 – NEI's (1972) standard genetic distance estimates between 9 samples of *Fejervarya* from Java (J), Kalimantan (K) and Sumatra (S) See text (*Material and methods*) for details on localities Sample Kc belongs to the species *Fejervarya cancrivora*

	J1	J2	K1	K3	S1	S2	S5	S6
J2	0 316							
K1	0 188	0 282						
K3	0 169	0 298	0 026					
S1	0 102	0 319	0 071	0 034				
S2	0 182	0 324	0 122	0 059	0 040			
S5	0 195	0 337	0 154	0 089	0 054	0 004		
S6	0 178	0 320	0 097	0 037	0 034	0 004	0 017	
Kc	1 198	1 088	0 968	0 974	1 021	0 957	0 970	0 953

Table 2 – Variable bp positions of a partial sequence of the mitochondrial 16S-rRNA gene of nine *Fejervarya* and three outgroup taxa haplotypes.

```
                     000000000000000000111111111111111111222222222222222222222222222222222
                     112445556667788888004446888889999999000000001111111112222222222333333
                     580074673586725678143574145781346789012346780123467890123456789123456

Fejervarya J2 B      CGCATAGGACGCCACCTCTCGTACCATAGACCAATCAACACACTATCTAATTCTTTCTCCCCCGCTTT
Fejervarya J2-A      -.....  ..     .  .  . ..                                  .
Fejervarya J2-C                                                                          .
Fejervarya J1-A         .  .  . T.GT....TAA.....GACT.G.CT..TCT..C.ATACC..   AAGTT    TCA
Fejervarya J1-B            .. T GT ...TAA.....GACT G.CT .TCT..C AAACC     AAGTT  - TCA
Fejervarya K1-A          ..   T GT    TAA     GACT.G.CT..TCT..C.AAACC..   AAGTT    TCA
Fejervarya K3-A        .   .. . T GT   .TAA     GACT.G.CT..TCT..C.AAACC..  .AAGTT  - TCA
Fejervarya S5-A        ......   T GT   .TAA     GACT G.CT .TCT .C.AAACC     AAGTT    TCA
Fejervarya S6-A      ...........T.GT....TAA.... GACT G CT  TCT  C AAACC     AAGTT -- TCA
F. cancrivora Kc     T..C.TAA...T.G...TC.T.C...CGA..TT.G CC T C CCCAA C     ACG      TCGC
Rana temporaria      .A.C.. ACTC.TG.TAT.TCA.GTCCC.CT.GTG.CC-T...CC.TA.CACAAGAGAT    A GGC
Rana catesbeiana     .A.CC.A.TTC..G.TATC.T...TTCTACT..TG CC-T-TA..A..TCACAAGAAA      TAGC

                     2222222222222222222223333333333333333333333333333333333333333333333
                     3556677778888889999990000111111223333333344444444445555556667 8
                     8386901391245682356780789234789590126789012345678147890180 0

Fejervarya J2 B      GTAACATT-CGCGTCA-TA-ACCAAGCCCGCGCGACTTGACGTTTTTTTTAATATTCAC
Fejervarya J2-A      ..............T .... . ...............................C.
Fejervarya J2 C
Fejervarya J1-A      .  CT A  T      C C CT TTA  ATT  A           GA          C
Fejervarya J1-B         CT A  T      C.C.CT.TTA..ATT. A.        G  A         T
Fejervarya K1-A         CT A  T    . .C.C.CT.TTA .ATT  A.         GA
Fejervarya K3 A         CT A  T     .C C CT.TTA  ATTT A          GA          G
Fejervarya S5-A         CT A  T      C C CT TTA  ATT  A          GA          GT
Fejervarya S6-A      ...CT.A..T......C.C.CT.TTA..ATT..A          GA          G
F. cancrivora Kc     ..G..T....AT..T.CCCTC...C...T....A...    AACAAA    T TC
Rana temporaria      AG.T T.ACTA.AAT-CA C....T.A.A...TACT      C  AN      A
Rana catesbeiana     AG.TTTAA.TA.AAT CA.C..T.C.ATAC..TACTC A T    AA  C  AT
```

Source : MNHN, Paris

Table 3 – Average substitution rate between samples of the two *Fejervarya* lineages J1 and J2 and three outgroup taxa, transitions and transversions were weighted equally, gaps treated as fifth base

	J1 lineage	J2 lineage	*F. cancrivora*	*R. temporaria*
J1 lineage (J/K/S)	0.006 ± 0.004			
J2 lineage	0.135 ± 0.004	0.006 ± 0.003		
F. cancrivora	0.160 ± 0.001	0.155 ± 0.001	-	
R. temporaria	0.219 ± 0.002	0.229 ± 0.001	0.210	-
R. catesbeiana	0.209 ± 0.002	0.212 ± 0.002	0.192	0.112

MORPHOMETRIC VARIATION

For all measurements and ratios, the mean, standard deviation and minimum and maximum values are given for adult specimens of *Fejervarya* separating samples by sex and geographical origin (app. 3). Comparisons of adult individuals using the Kruskal-Wallis test (tab. 4) show significant differences in the frogs from the three islands in the ratios which all concern head shape (head length, distance between anterior border of eyes, distance between posterior border of eyes, internarial distance). *Fejervarya* from Java have significantly shorter heads and more pointed snouts than the frogs from Sumatra and Borneo. Frogs from Sumatra are significantly distinct in having a greater distance between posterior border of eyes (app. 3, tab. 4).

Dorsal pattern

In the populations we studied, 32.1 % of the specimens have no mid-dorsal stripe, a fine mid-dorsal line is present in 57.6 % of all specimens examined, a wide stripe in 30.5 % of the specimens, and the combined fine-wide striped phenotype was observed in 15.3 % of the specimens (tab. 5).

More males lack a mid-dorsal line and more females have a combination of both phenotypes (chi-square test, $\chi^2 = 23.0181$, $df = 3$, $P < 0.001$). Neither males nor females differ in a significant manner from the overall distribution of dorsal pattern (chi-square test: males, $\chi^2 = 5.7635$, $df = 3$, $P > 0.05$; females, $\chi^2 = 5.1466$, $df = 3$, $P > 0.05$).

The different populations can be put in three groups: a series of populations showing no wide stripe phenotypes (group 1 in table 5), a population from Sumatra showing no narrow line pattern (group 3 in table 5), and a group of populations showing all four patterns (group 2 in table 5). Statistical test shows heterogeneity of phenotype distribution for the wide stripe pattern between populations studied (Kruskal-Wallis test, $\chi^2 = 22.38$, $df = 7$, $P < 0.01$). Distribution between populations for narrow line pattern is not statistically heterogeneous (Kruskal-Wallis test: $\chi^2 = 12.05$, $df = 7$, $P > 0.05$). The population from Chianjur is in the

Source : MNHN, Paris

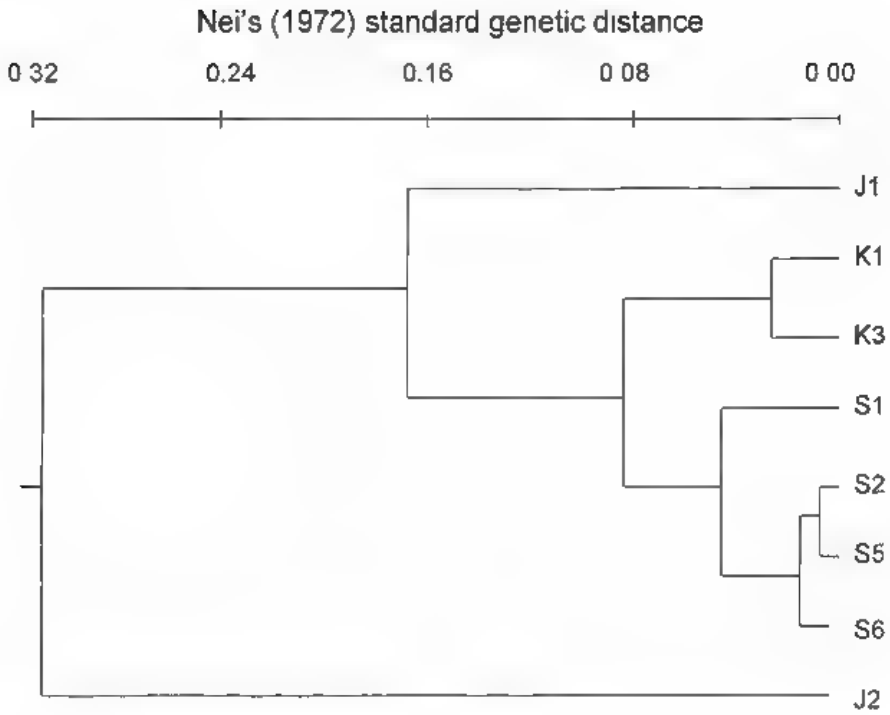

Fig 3 – UPGMA phenogram of Nei's (1972) standard genetic distances between the *Fejervarya* samples (allozyme data), the tree is rooted by the outgroup *Fejervarya cancrivora*; the cophenetic value is 0 99

same dorsal pattern group as the population from Desa Lape (Borneo) and the population from Medan (Sumatra) The two Javanese populations are not in the same dorsal pattern group.

In conclusion, populations of *Fejervarya* from the Sunda Islands show statistically significant variation of dorsal colour patterns, but this variation is not congruent with allozyme or mtDNA variation as shown in this study.

To which population does the name Rana limnocharis *Gravenhorst, 1829 apply?*

The name-bearing type provides the objective standard of reference by which the application of the name it bears is determined (Anonymous, 1999: Article 61.a) Generally, taxa have been described using morphological methods, and new techniques are rarely applicable to dead museum specimens. Systematics is, however, a largely historical science, as new results are added to previous knowledge. One scope of modern science therefore is to define methods to find quantifiable links between historical museum specimens (especially type-specimens) and new material studied by modern methods.

Multivariate statistics have been used to refer single type specimens to biologically defined populations (Heyer, 1994, Ohler, 1996, 1999, Ohler & Dubois,1999) This also applies to the case of the two *Fejervarya* lineages here defined by allozyme and DNA data.

The historical specimen of Heinrich Kuhl, who first collected the species *Rana limnocharis*, was a judicious choice for a neotype (see Dubois & Ohler, 2000) In order to find out to

Source : MNHN, Paris

Table 4 – Comparison by Kruskal Wallis test of snout-vent length (SVL) and of ratios of measurements in adult specimens of *Fejervarya* from different origins. For each sample, minimum and maximum values, mean and standard deviation are given. *df*, degree of freedom, *n* sample size, *P*, probability, *, significance level $P \leq 0.05$

	Java *n* = 3	Sumatra *n* = 17	Kalimantan *n* = 14	Kruskall-Wallis test *df* = 2
FL / SVL	96 – 117 108 ± 10.6	97 – 129 112 ± 8.59	109 – 126 115 ± 4.60	χ^2 = 2.783 *P* = 0.249 *ns*
FN / SVL	86 – 91 88 ± 2.55	80 – 101 91 ± 5.45	81 – 95 89 ± 4.70	χ^2 = 2.010 *P* = 0.366 *ns*
FLL / SVL	196 – 221 209 ± 12.6	191 – 227 215 ± 9.12	207 – 230 221 ± 6.80	χ^2 = 5.259 *P* = 0.072 *ns*
FOL / SVL	496 – 554 523 ± 29.2	490 – 563 533 ± 20.4	465 – 560 530 ± 24.1	χ^2 = 0.576 *P* = 0.750 *ns*
FTL / SVL	303 – 324 316 ± 11.6	292 – 338 319 ± 14.4	273 – 344 319 ± 16.8	χ^2 = 0.407 *P* = 0.816 *ns*
HAL / SVL	176 – 221 199 ± 22.5	173 – 219 197 ± 13.2	180 – 223 203 ± 12.0	χ^2 = 1.601 *P* = 0.449 *ns*
HL / SVL	329 – 375 356 ± 24.1	369 – 448 388 ± 17.8	363 – 416 391 ± 14.5	χ^2 = 6.849 *P* = 0.033 *
HW / SVL	342 – 360 350 ± 9.34	332 – 365 347 ± 10.3	319 – 367 348 ± 13.3	χ^2 = 0.268 *P* = 0.875 *ns*
IBE / SVL	210 – 246 232 ± 18.8	208 – 249 225 ± 11.5	217 – 271 238 ± 14.8	χ^2 = 6.668 *P* = 0.036*
IFE / SVL	129 – 145 138 ± 8.60	135 – 162 147 ± 8.87	141 – 173 156 ± 10.1	χ^2 = 8.680 *P* = 0.013*
IMT / SVL	44 – 56 50 ± 6.26	45 – 57 51 ± 3.21	46 – 57 51 ± 3.49	χ^2 = 0.542 *P* = 0.762
IN / SVL	66 – 69 68 ± 1.58	68 – 79 73 ± 3.13	66 – 85 75 ± 4.69	χ^2 = 7.739 *P* = 0.021 *
ITL / SVL	96 – 126 108 ± 15.4	103 – 123 116 ± 4.95	108 – 125 118 ± 5.38	χ^2 = 2.148 *P* = 0.342
MBE / SVL	140 – 154 145 ± 8.1	137 – 171 149 ± 11.0	135 – 193 158 ± 17.3	χ^2 = 2.840 *P* = 0.242 *ns*
MFE / SVL	221 – 255 237 ± 17.5	226 – 294 249 ± 16.0	229 – 279 252 ± 14.7	χ^2 = 1.746 *P* = 0.418 *ns*
MN / SVL	306 – 326 314 ± 10.7	310 – 393 330 ± 19.2	304 – 373 335 ± 16.2	χ^2 = 5.339 *P* = 0.069 *ns*
SVL	44.4 – 55.2 48.4 ± 5.91	32.6 – 59.0 48.6 ± 8.36	36.2 – 54.2 46.1 ± 6.06	χ^2 = 1.458 *P* = 0.482 *ns*
TEL / SVL	114 – 130 123 ± 7.97	102 – 130 118 ± 6.76	105 – 135 123 ± 7.84	χ^2 = 4.216 *P* = 0.121 *ns*
TL / SVL	489 – 532 504 ± 23.9	475 – 537 514 ± 17.1	465 – 534 508 ± 16.9	χ^2 = 1.772 *P* = 0.412 *ns*
TYD / SVL	63 – 66 65 ± 1.86	58 – 69 63 ± 3.33	59 – 73 66 ± 4.05	χ^2 = 5.454 *P* = 0.065 *ns*
TYE / SVL	35 – 40 37 ± 2.45	32 – 44 39 ± 3.32	27 – 49 40 ± 4.74	χ^2 = 1.408 *P* = 0.495
WEE / SVL	73 – 102 83 ± 16.5	63 – 92 77 ± 8.26	52 – 97 78 ± 12.2	χ^2 = 0.207 *P* = 0.902 *ns*
WI / SVL	75 – 87 82 ± 5.9	65 – 88 77 ± 7.39	63 – 92 79 ± 8.78	χ^2 = 1.083 *P* = 0.582
WII / SVL	55 – 79 64 ± 12.7	40 – 75 60 ± 8.97	46 – 79 60 ± 9.49	χ^2 = 0.222 *P* = 0.895 *ns*
WIF / SVL	86 – 108 96 ± 11.2	74 – 100 87 ± 8.69	77 – 104 90 ± 8.07	χ^2 = 2.713 *P* = 0.258 *ns*

Source MNHN, Paris

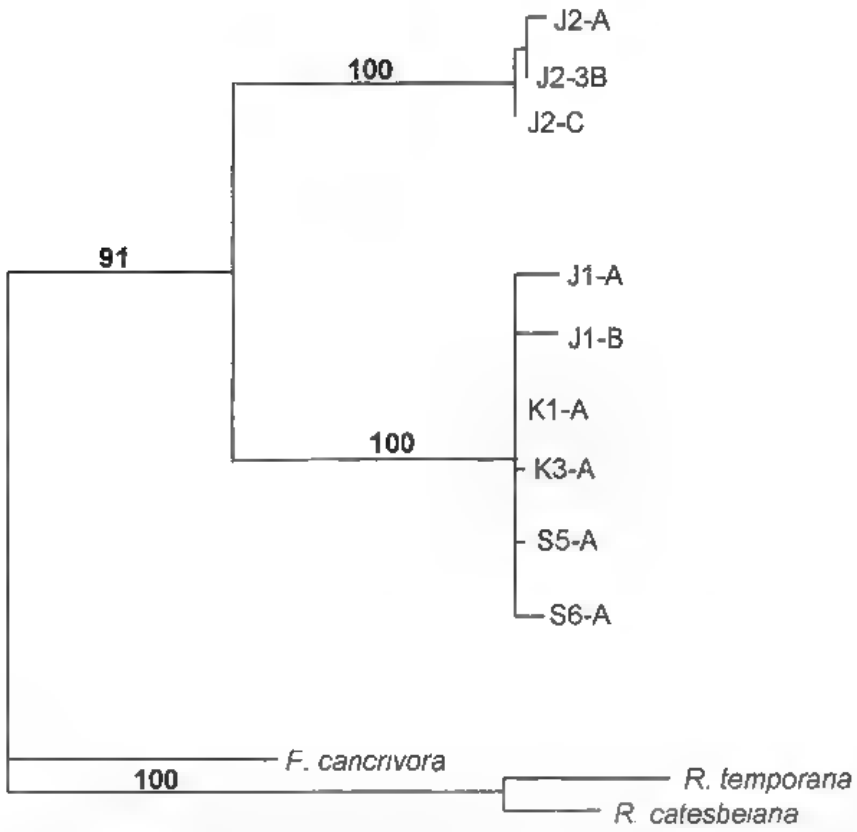

Fig. 4 — Maximum parsimony tree of 390 bp of the mitochondrial 16S rRNA gene of nine *Fejervarya* haplotypes. Tree length is 202 steps (one shortest tree only), bootstrap values > 50 % for 1000 replicates are indicated

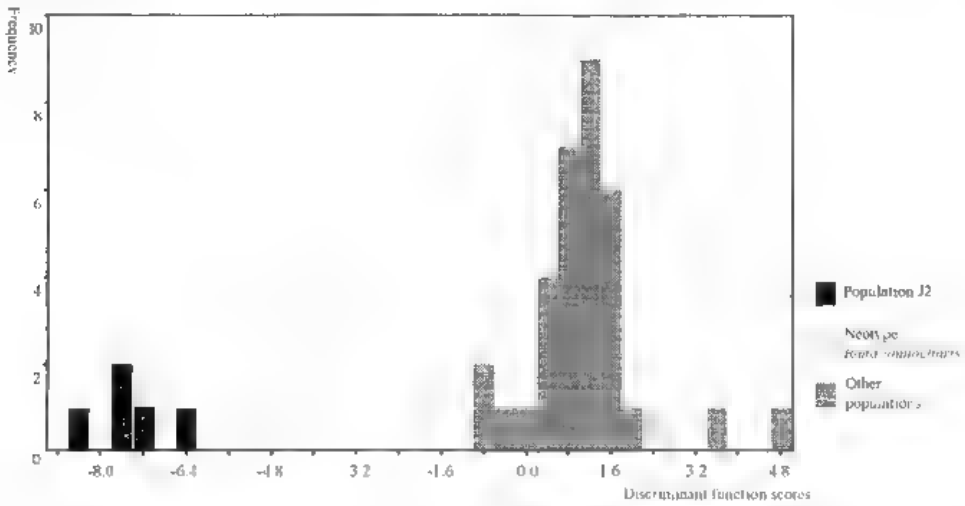

Fig. 5 — Stacked histogram of discriminant function for specimens of population J2 and other populations of *Fejervarya* from Sunda Islands. The neotype RMNH 4287 of *Rana limnocharis* Gravenhorst, 1829 was included into this analysis without a priori group membership

Source : MNHN, Paris

Table 5 Coloration pattern of dorsum in *Fejervarya* from Sunda Islands Frequency distribution of phenotypes of mid-dorsal line and alleles supposed present in populations studied n, allele wild narrow line, N, allele narrow line, w, allele wild wide line, W, allele wide line Proposed phenotypical groups 1, line absent or narrow line present (wide line never observed), 2, line absent or fine and or wide line present (all 4 phenotypes observed), 3, line absent or wide line present (fine line never observed)

Sample (sample size)	Line absent	Fine line	Wide line	Fine and wide line	Alleles inferred to be present in genotype	Proposed group
J1 Bogor (4)	2	2	0	0	n, N / w	1
S2 Sidikalang (2)	1	1	0	0	n, N / w	1
S5 Tapaktuan (5)	2	3	0	0	n, N / w	1
S6 Desa Seleutkat (3)	2	1	0	0	n, N / w	1
S1 Medan (13)	1	10	0	2	n, N / w, W	2
J2 Chianjur (11)	5	3	1	2	n, N / w, W	2
K3 Desa Lape (13)	2	2	6	3	n, N / w, W	2
K1 Pontianak (2)	0	0	2	0	n / w, W	3

which genetically defined lineage (population J2 or the other populations from Sunda Islands) this name applies, a discriminant analysis was performed and subsequently applied to the neotype of *Rana limnocharis*. The analysis clearly classes the neotype with lineage J1 and not with the specimens from population J2 (tab. 6, fig. 5). This indicates that the name *Rana limnocharis* Gravenhorst, 1829 should apply to the widely distributed taxon occurring in Java, Sumatra and Borneo, and that a new name should be created for the species from population J2. As no other name is available for this taxon (see DUBOIS & OHLER, 2000), we describe it as a new species. The morphological comparison of adult males of the new species and *Fejervarya limnocharis* is summarised in table 7.

Fejervarya iskandari sp. nov.

Diagnosis Medium sized *Fejervarya* with a relatively wide head and interorbital distance, small tympanum, short eye length, short forearms, short inner toes and small inner metatarsal tubercles.

Description of holotype MNHN 1997 4916, adult male (fig. 2a), from paddy field at Chianjur (Java) (6°12'S, 107°08'E).

(A) Size and general aspect (1) Specimen of rather small size (SVL 40.4 mm), body moderately stout.

Source : MNHN, Paris

Table 6 – Results of canonical discriminant analysis between genetically determinated specimens of *Fejervarya*

A Statistical significance

Eigenvalue	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	*P*
8.7871	0.9475	0.102175	52.465	26	0.0016

B Standardised canonical discriminant function coefficients

Morphometric character	Function 1
EL	1.86131
EN	– 3.16796
FLL	1.38762
FOL	0.52334
FTL	– 6.44177
HAL	– 0.01355
HL	– 11.18890
HW	– 1.91388
IBE	– 3.85940
IFE	2.55580
IN	1.88979
ITF	– 0.99019
IUE	– 0.29879
MBE	– 3.25966
MFE	5.56794
MN	4.88480
SVL	42.020
TFL	1.21313
TL	7.26577
TYD	2.31338
TYE	1.93537
UEW	0.69464
WFE	0.54972
WI	1.86954
WIE	– 0.75687
WIT	– 0.96165

C Classification success.

Actual group	Predicted group	
	F. iskandari	*F. limnocharis*
Fejervarya iskandari	5 (100 %)	0
Fejervarya limnocharis	0	33 (100 %)
Neotype of *Rana limnocharis* (ungrouped)	0	1 (100 %)

Source : MNHN, Paris

Table 7 Comparison of adult males of *Fejervarya iskandari* sp. nov and *Fejervarya limnocharis* (Gravenhorst, 1829) by Mann-Whitney *U* test *n*, sample size, *P*, probability, *U*, Mann-Whitney *U*, *ns*, significance level P > 0 05, **, significance level $P \leq 0\ 01$

Variable	*F. iskandari* *n* = 5	*F. limnocharis* *n* = 7	Mann-Whitney *U* test
EL / SVL	106 ± 2.89 102 – 109	120 ± 6.87 112 – 129	*U* = 0 *P* = 0 0045 **
EN / SVL	94 ± 4.75 88 – 99	91 ± 6.81 82 – 101	*U* = 14 *P* = 0 5698 *ns*
FLL / SVL	209 ± 6.12 199 – 215	222 ± 4.36 218 – 230	*U* = 0 *P* = 0 0045**
FOL / SVL	524 ± 27 16 489 – 557	536 ± 12.62 522 – 557	*U* = 14 *P* = 0 5698 *ns*
FTL / SVL	323 ± 13 44 308 – 337	324 ± 8.37 315 – 337	*U* = 16 *P* = 0 8075 *ns*
HAL / SVL	212 ± 8.74 200 – 224	203 ± 15.74 179 – 223	*U* = 11 *P* = 0 2912 *ns*
HL / SVL	395 ± 17.18 374 – 416	397 ± 23.56 375 – 447	*U* = 17 *P* = 0.9353 *ns*
HW / SVL	358 ± 12 337 – 367	348 ± 5.96 340 – 354	*U* = 7 *P* = 0.0882 *ns*
IBE / SVL	239 ± 5 54 232 – 245	244 ± 16.43 221 – 273	*U* = 13 *P* = 0 4649 *ns*
IFE / SVL	152 ± 10.67 141 – 162	157 ± 7 52 144 – 168	*U* = 14 *P* = 0 5698 *ns*
IMT / SVL	44 ± 3 19 43 – 48	50 ± 2.8 46 – 53	*U* = 1 *P* = 0.0526 *ns*
IN / SVL	74 ± 1.68 72 – 76	76 ± 4.73 71 – 85	*U* = 15 *P* = 0.6847 *ns*
ITL / SVL	110 ± 10 1 96 – 124	119 ± 3.92 113 – 124	*U* = 7 *P* = 0 0882 *ns*
IUE / SVL	54 ± 2.41 50 – 56	50 ± 3.78 46 – 55	*U* = 7 *P* = 0 0882 *ns*
MBE / SVL	163 ± 20.53 138 – 188	153 ± 14.13 134 – 171	*U* = 12 *P* = 0.3718 *ns*
MFE / SVL	255 ± 19 8 234 – 275	255 ± 19.62 237 – 294	*U* = 16 *P* = 0 8075 *ns*
MN / SVL	340 ± 19 07 318 – 360	339 ± 25 19 320 – 393	*U* = 16 *P* = 0 8075 *ns*
SVL	417 ± 11 37 404 – 427	398 ± 54 6[illegible] 326 – 467	[illegible] *P* = 0.5691 *ns*
TFL / SVL	124 ± 11 21 111 – 136	123 ± 4.9 118 – 132	*U* = 15 *P* = 0 6847 *ns*
TI / SVL	494 ± 17 51 468 – 511	507 ± 12 76 488 – 523	*U* = 8 *P* = 0 1229 *ns*
TYD / SVL	67 ± 2.87 63 – 70	65 ± 5.34 59 – 73	*U* = 14 *P* = 0 5698 *ns*
TYE / SVL	33 ± 2 93 31 – 38	38 ± 4 29 32 – 43	*U* = 7 *P* = 0 0882 *ns*
UEW / SVL	83 ± 5.98 76 – 88	91 ± 4 67 87 – 100	*U* = 7 *P* = 0.0882 *ns*
WFE / SVL	81 ± 10 69 69 – 98	80 ± 11 63 61 – 97	[illegible] 17 [illegible] 0 9353 [illegible]
WI / SVL	76 ± 12.99 64 – 96	81 ± 8.2 69 – 92	*U* = 12 *P* = 0 3718 *ns*
WIE / SVL	62 ± 12 11 47 – 80	61 ± 10 8 46 – 79	*U* = 15 *P* = 0 6847 *ns*
WTF / SVL	87 ± 12.03 76 – 106	92 ± 6.31 82 – 99	*U* = 10 *P* = 0 2232 *ns*

Source : MNHN, Paris

(B) Head. (2) Head of medium size, longer (HL 15.4 mm) than wide (HW 14.4 mm; MN 13 1 mm; MFE 9.5 mm; MBE 5 9 mm), convex. (3) Snout pointed, protruding, its length (SL 7.90 mm) much longer than horizontal diameter of eye (EL 4.34 mm) (4) Canthus rostralis rounded, loreal region very concave, vertical. (5) Interorbital space flat, smaller (IUE 2 27 mm) than upper eyelid (UEW 3 57 mm) and internarial distance (IN 2.92 mm); distance between front of eyes (IFE 5.7 mm) about half of distance between back of eyes (IBE 9 5 mm) (6) Nostrils oval with flap of skin laterally, closer to tip of snout (NS 3 55 mm) than to eye (EN 4 02 mm). (7) Pupil rounded. (8) Tympanum (TYD 2.72 mm) distinct, rounded, more than half of eye diameter; tympanum-eye distance (TYE 1.30 mm) about half its diameter (9) Pineal ocellus present, between anterior border of eyes. (10) Vomerine ridge present, bearing few small teeth, between choanae, with an angle of 45° to body axis, less close to choanae than from each other, longer than distance between them. (11) Tongue large, rounded, emarginate (12) Supratympanic fold distinct, from eye to shoulder. (13) Parotoid glands absent. (14) Cephalic ridges absent. (15) Co-ossified skin absent.

(C) Forelimbs. – (16) Arm short, rather thin (FLL 8.7 mm), as long as hand (HAL 8.7 mm), not enlarged (17) Fingers I, III and IV long, finger II short, all thin (TFL 5 32 mm) (18) Relative length of fingers, shortest to longest: II < IV < I < III. (19) Tips of fingers pointed. (20) Finger II with dermal fringe; webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present (22) Prepollex oval, prominent; two oval, distinct palmar tubercles; supernumerary tubercles absent.

(D) Hindlimbs. - (23) Shank three times longer (TL 20 6 mm) than wide (TW 6 0 mm), longer than thigh (FL 18 8 mm), but shorter than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 22 5 mm) (24) Toes long, thin; toe IV long (FTL 13.6 mm), more than one third of distance from base of tarsus to tip of toe IV (TFOL 29.6 mm). (25) Relative length of toes, shortest to longest: I < II < V < III < IV (26) Tips of toes pointed (27) Webbing moderate I 1 2 II 1 – 2 III 1 - 2 2/3 IV 2 1/3 – 1 V (WTF 4.28 mm; WFF 3.95 mm; WI 3 89 mm; WII 3 24 mm, MTTF 9.7 mm; MTFF 10 3 mm; TFTF 9 5 mm; FFTF 10 0 mm) (28) Dermal fringe along toe V present, from tip of toe to base of metatarsus, well developed. (29) Subarticular tubercles prominent, oval, simple, all present (30) Inner metatarsal tubercle long, very prominent, its length (IMT 1.94 mm) less than 2.5 times in length of toe I (ITL 4.60 mm). (31) Inner tarsal ridge well developed, along distal half of tarsus. (32) Outer metatarsal tubercle prominent, supernumerary tubercles absent, tarsal tubercle absent.

(E) Skin. – (33) Dorsal and lateral parts of head and body, snout smooth, between the eyes and side of head with few, flat glandular warts; back with glandular folds and glandular warts between them, flanks with glandular warts. (34) Latero-dorsal folds absent (35) Dorsal parts of limbs forelimbs smooth; shank, thigh and tarsus with glandular warts. (36) Ventral parts of head, body and limbs: throat, chest and belly smooth, thigh with glandular warts. (37) No macroglands.

(F) Coloration in alcohol (38) Dorsal and lateral parts of head and body brown with blackish paired spots, shoulder spots indistinct, four brown spots on each side of upper lip (39) Dorsal parts of limbs forelimb, thigh, shank and foot light brown with dark bands, posterior part of thigh with brown and whitish marbling (40) Ventral parts of head, body and limbs chest, belly and thigh cream white; throat cream white with grey W-shaped pattern, margin of throat white with large brown spots.

Source : MNHN, Paris

(G) Male sexual characters. – (41) Nuptial spines in one single patch on prepollex and finger I; numerous, indistinct, cream coloured spines. (42) Vocal sacs as greyish, folded skin on the two sides of the throat; slit-like openings in rather anterior part of mouth floor. (43) Fine horny spinules on the anterior border of the throat.

(H) Part of the 16S rRNA sequence that corresponds to the nucleotides 3994-4554 of *Xenopus laevis* (ROE et al., 1985) – (44) (EMBL AJ292018) TCTTGTTTTTTCATAA GAGGTCCAGCCTGCCCAGTGACACAATTAAAGGCCGCGGTACCCTGACCGTG CGAAGGTAGCATAATAACTTGTTCTTTAAATGGGGACTAGCATGAACGGCAC CACGAAGGCCTCACTGTCTCCTTTTTCCAATCAGTGAAACTGATCTCCCCGTG AAGAAGCGGGGATGATAATATAAGACGAGAAGACCCCATGGAGCTTTAAACC CAATAAGCAACCCTAATCAACACAACTCATCTAAATTCTTTCTCCCCCTGCTTT TTGGTTTTAGGTTGGGGTGACCACGGAGTAAAACATATCCTCCACGACGTAC GGATTAACCCTTATCCAAGAGCCACCGCTCTAAGAATCGACAAATTGACGTTT TTTGATCCAATATATTGATCAACGAACCAAGTTACCCTGGGGATAACAGCGCA ATCCATTTTTAGAGCCCCTATCGACGAATGGGTTTACGACCTCGATGTTGGAT CAGGGTACCCAAGTGGTGCAGCCGCTACTAATGGTTTGTTTGTTCAACAATT AAAACCCTACGTGATCTGAGTTC.

Paratopotypes. – FMNH 256725-256733, 3 adult males, 1 adult female, 5 juvenile males; ZFMK 68867, adult male. Same collection data.

Etymology. – The new species is dedicated to Djoko Iskandar, herpetologist from Indonesia

DISCUSSION

Fejervarya iskandari sp. nov. and *Fejervarya limnocharis* (Gravenhorst, 1829) from Java clearly represent two genetically distinct lineages. Their Nei D values calculated from allozyme data (average 0.314) falls within the interspecific range known from other ranids (e.g., CASE, 1978, NISHIOKA & SUMIDA, 1990; MENSI et al., 1992; ARANO et al., 1993; BIERLI et al., 1996, VEITH, 1996). However, the observed morphological variation between the genetically well differentiated lineages *F. iskandari* and *F. limnocharis* is slightly more pronounced than among members of the other populations, as estimated by the number of significantly distinct measurements. Therefore these two forms are clearly a pair of sibling species that are morphologically scarcely distinct from one another, but show substantial genetic differentiation. In addition, a comparison of our allozyme data with those of the samples 3 and 4 of TODA et al. (1998*a*) reveals that their samples fit almost perfectly with our analysis: in nine out of eleven loci which were analysed in both studies the results are identical, one locus shows similar allele frequencies and only in one locus the results are different. Discrepancies in the results may have been caused by using different protocols in the two laboratories (see VEITH, 1994 for further examples). Therefore the new species includes specimens from the Javanese populations of Chianjur and Malingping (sample 4 in TODA et al., 1998*a*). It is genetically well defined, but morphologically very similar to *F. limnocharis*. Distribution ranges of *F. iskandari* and *F. limnocharis* overlap at least between Malingping and Chianjur over a distance of ca. 130 km. Syntopy was shown for a paddy field near Malingping, Java (TODA et al., 1998*a*), confirming species status of *F. iskandari*.

Source : MNHN, Paris

Discriminant analysis of morphometric data resolves the nomenclatural relevance of the observed genetic divergence. The name *Rana limnocharis* Gravenhorst, 1829 applies to a taxon widely distributed in the Sunda Islands. As there is no indication of genetic or morphological differentiation of the frogs from Borneo island, the name *Rana wasl* Annandale, 1917 (based on a holotype from Kuching, Sarawak, Malaysia, on this island) is here considered a junior subjective synonym of *Rana limnocharis* (see DUBOIS & OHLER, 2000), but remains available for further systematic decisions, should Bornean *Fejervarya* prove heterogeneous.

RÉSUMÉ

Les grenouilles de l'espèce *Fejervarya limnocharis* et d'espèces voisines de celle-ci sont parmi les plus communes en Asie du Sud-Est. Nous avons étudié 52 spécimens de huit populations des Iles de la Sonde par les méthodes de l'électrophorèse d'allozymes, du séquençage d'ADN mitochondrial et de la morphométrie. Les patrons de variation de tous les caractères entre les populations se montrent congruents pour séparer une population de Java de toutes les autres populations (Java, Sumatra, Bornéo) et considérer qu'elle appartient à une espèce distincte. Les fréquences des quatre phénotypes observes concernant la présence et la largeur d'une ligne médio-dorsale dans les populations examinées ne permettent pas de dégager de claire corrélation avec les caractères moléculaires et morphométriques. Notre analyse morphométrique permet d'attribuer sans ambiguïte le nom *Rana limnocharis* Gravenhorst, 1829 à l'espèce à vaste répartition qui se trouve à Java, Sumatra et Bornéo. Les deux taxa vivant en sympatrie, nous donnons un nom nouveau, *Fejervarya iskandari*, à la population de Chianjur, Java.

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Source : MNHN, Paris

Appendix 1 List of morphometric measurements of *Fejervarya* specimens used in this study.

Abbreviation	Measurement
EL	eye length
EN	distance from front of eye to nostril
FFTF	webbing measured from maximum incurvation between toes IV and V to tip of toe IV
FLL	length of arm from elbow to base of outer palmar tubercle
FOL	length of foot from proximal border of inner metatarsal tubercle to tip of toe IV
FTL	length of fourth toe from basal border of proximal subarticular tubercle to tip of toe IV
HAL	length of hand from base of outer palmar tubercle to tip of finger III
HL	head length from mandibular articulation to tip of snout
HW	head width
IBE	distance between posterior borders of eyes
IFE	distance between anterior borders of eyes
IMT	length of inner metatarsal tubercle
IN	internarial distance
ITL	inner toe length from distal border of inner metatarsal tubercle to tip of toe I
MBE	distance from mandibular articulation to posterior border of eye
MFE	distance from mandibular articulation to anterior border of eye
MN	distance from mandibular articulation to nostril
MTFF	webbing measured from distal border of inner metatarsal tubercle to maximum incurvation between toes IV and V
MTTF	webbing measured from distal border of inner metatarsal tubercle to maximum incurvation between toes III and IV
SVL	snout-vent length
TFL	length of finger from basal border of proximal subarticular tubercle to tip of finger III
TFTF	webbing measured from maximum incurvation between toes III and IV to tip of toe IV
TL	length of tibia from tibio-metatarsal articulation to knee
TYD	maximum tympanum diameter
TYE	tympanum-eye distance

Source : MNHN, Paris

Appendix 2 Allele frequencies, average expected heterozygosity (H_e) and polymorphism (P) at 15 presumptive enzyme loci in 9 samples of *Fejervarya* from Java (J), Kalimantan (K) and Sumatra (S) See text (*Material and methods*) for details on localities Sample Kc belongs to the species *Fejervarya cancrivora*

Sample (n)	J1 (3)	J2 (11)	K1 (2)	K3 (12)	S1 (13)	S2 (2)	S5 (5)	S6 (3)	Kc (25)
ACON-1	a	b	a	a	a	a	a	a	a
ACON-2	b	a	b	b	b	b	b	b	c
FUM	a	a	a	a	a	a	a	a	a
AAT-1	c	a (0.05) c (0.90) d (0.05)	c	b (0.04) c (0.96)	c	c	c	c	e (0.02) f (0.98)
AAT-2	a	b	a (0.25) b (0.75)	a (0.70) b (0.30)	a	a	a	a	c
IDH-1	a	a	a	a	a	a	a	a	b
IDH-2	a	a	a	a	a	a	a	a	a (0.96) b (0.04)
LDH	a	b	a	a	a	a	a	a	c
MDH	a (0.87) b (0.13)	a	c	c (0.96) d (0.04)	b (0.09) c (0.50) d (0.41)	c (0.25) d (0.75)	d	c (0.50) d (0.50)	e
ME	a	a	a	a	a	a	a	a	b
MPI	d	b (0.59) c (0.41)	a (0.25) c (0.50) e (0.25)	a (0.25) b (0.45) d (0.25) e (0.05)	b (0.35) d (0.65)	b	b	b	b (0.60) f (0.14) g (0.26)
PEP (Gly-Leu)	b (0.37) c (0.63)	a	b	b	a (0.15) b (0.85)	b	b	b	b
PGM	a	a	a	a (0.84) b (0.16)	a (0.88) b (0.12)	a	a	a	c
PK	a	a	a	a	a	a	a	a	b
TPI	b (0.87) c (0.13)	b (0.95) c (0.05)	a (0.25) b (0.50) c (0.25)	a (0.05) b (0.95)	b	b	b	b	b
H_e	0.06	0.05	0.11	0.15	0.1	0.02	0	0.03	0.04
P	0.2	0.2	0.2	0.4	0.26	0.06	0	0.06	0.2

Source MNHN, Paris

Appendix 3 – Morphometrical data for adult specimens of *Fejervarya* samples from Sunda Islands Mean, standard deviation, minimum and maximum values are given for all samples

Measurement or ratio	Chianjur (Java) 5 males	Medan (Sumatra) 2 males	Desa Seleukat (Sumatra) 1 male	Desa Lape (Kalimantan) 4 males	Bogor (Java) 1 female	Chianjur (Java) 1 female	Medan (Sumatra) 7 females
EL / SVL	106 ± 2.89 102 – 109	119 ± 10.37 112 – 127	129	119 ± 5.19 114 – 126	96	111	107 ± 6.03 97 – 115
EN / SVL	94 ± 4.75 88 – 99	98 ± 4.65 95 – 101	91	87 ± 6 82 – 95	86	87	92 ± 4.83 87 – 100
FLL / SVL	209 ± 6.12 199 – 215	222 ± 4.56 219 – 226	221	222 ± 5.52 218 – 230	221	2[illegible]1	2[illegible]9 ± 9.46 191 - 218
LOL / SVL	524 ± 27.16 489 – 557	543 ± 7.87 538 – 549	528	535 ± 15.47 522 - 557	496	5[illegible]8	524 ± 22.68 490 - 548
TTL / SVL	323 ± 13.44 308 – 337	319 ± 5.44 315 – 323	337	324 ± 7.37 315 - 333	303	320	309 ± 13.[illegible]4 292 – 325
HAL / SVL	212 ± 8.74 200 – 224	192 ± 17.68 179 - 204	215	206 ± 15.82 186 - 223	176	200	195 ± 10.49 176 – 210
HL / SVL	395 ± 17.18 374 – 416	415 ± 45.75 383 - 447	399	388 ± 9.21 375 - 395	375	364	382 ± 5.85 374 - 389
HW / SVL	358 ± 12 337 – 367	351 ± 4.96 347 - 354	353	345 ± 6.21 340 - 354	348	342	350 ± 13.19 332 - 365
IBI / SVL	239 ± 5.54 232 – 245	235 ± 19.81 221 - 249	248	247 ± 18.43 231 – 273	210	239	224 ± 7.84 212 – 236
IRE / SVL	152 ± 10.67 141 – 162	157 ± 6.72 153 – 162	160	157 ± 9.77 144 – 168	129	145	148 ± 8.41 137 – 162
IMT / SVL	44 ± 3.19 43 – 48	51 ± 1.67 50 – 53	–	50 ± 3.56 46 – 53	56	44	53 ± 3.21 48 – 57
IN / SVL	74 ± 1.68 72 – 76	75 ± 1.96 73 – 76	72	78 ± 5.7 71 – 85	66	68	74 ± 2.87 70 – 79
ITL / SVL	110 ± 10.1 96 – 124	117 ± 5.35 113 – 120	119	119 ± 4.21 114 – 124	96	102	115 ± 5.64 103 – 122
IUE / SVL	54 ± 2.41 50 - 56	50 ± 6.09 46 - 55	52	50 ± 3.93 46 – 54	46	50	48 ± 3.51 40 – 51
MBF / SVL	163 ± 20.53 138 - 188	154 ± 24.04 137 – 171	147	154 ± 13.9 134 – 167	154	140	145 ± 7.23 138 – 159
MTL / SVL	255 ± 19.8 234 - 275	266 ± 40.71 237 – 294	26[illegible]	249 ± 9.31 237 - 260	255	235	243 ± 9.28 232 – 254
MN / SVL	340 ± 19.07 318 – 360	360 ± 46.64 327 – 393	337	329 ± 9.97 320 – 341	326	309	323 ± [illegible].99 310 – 341
SVL	41.7 ± 1.14 40.4 – 42.7	39.3 ± 8.42 33.3 – 45.2	32.6	41.9 ± 3.53 38.1 – 46.7	55.2	45.6	54.7 ± 2.53 51.7 – 59.0
TFL / SVL	124 ± 11.21 1[illegible]1 – 136	120 ± 2.17 119 – 122	123	124 ± 6.23 118 – 132	114	124	114 ± 7.05 102 – 123
TL / SVL	494 ± 17.5 468 - 511	516 ± 2.96 514 – 518	494	507 ± 14.72 488 – 523	489	491	514 ± 20.85 475 – 537
TYD / SVL	67 ± 2.87 63 – 70	65 ± 4.57 62 – 68	60	67 ± 5.93 59 – 73	66	63	62 ± 4.1 58 – 67
TY / SVL	33 ± 2.93 3[illegible] - 38	35 ± 5.22 32 – 39	34	40 ± 3.64 37 – 43	38	[illegible]	37 ± 2.61 35 – 42
[illegible]W / SVL	83 ± 5.98 76 – 88	89 ± 2.83 87 – 91	9[illegible]	91 ± 6.27 87 – 100	80	75	86 ± 3.06 82 – 92
WFF / SVL	81 ± 10.69 69 – 98	80 ± 3.05 77 – 82	91	78 ± 14.69 61 - 97	75	72	78 ± 8.36 63 – 85
WL / SVL	7[illegible] ± 12.99 [illegible]4 – 96	83 ± 3.78 80 - 86	87	78 ± 9.91 69 – 92	75	87	7[illegible] ± 7.57 66 – 88
WIE / SVL	62 ± 12.11 47 – 80	56 ± 2.76 54 – 58	70	60 ± 13.86 46 – 79	59	55	5[illegible] ± 2.19 4[illegible] – 65
WTI / SVL	87 ± 12.03 76 – 106	94 ± 4.94 90 – 97	99	90 ± 6.79 82 – 98	86	95	85 ± 6.83 78 – 98

Source : MNHN, Paris

Appendix 3. – Continued

Measurement or ratio	Sidikalang (Sumatra) 1 female	Tapaktuan (Sumatra) 4 females	Desa Seleukat (Sumatra) 2 females	Desa Lape (Kalimantan) 8 females	Pontianak (Kalimantan) 2 females	Java *R. limnocharis* neotype 1 female
EL / SVL	104	116 ± 4 73 111 – 121	108 ± 1 04 107 – 109	113 ± 3 97 109 – 120	116 ± 2 7 114 – 118	117
EN / SVL	80	89 ± 4 04 85 – 93	89 ± 2 34 87 – 91	88 ± 3 93 81 – 91	94 ± 1 07 94 95	91
FLL / SVL	208	217 ± 5 77 212 – 225	224 ± 3 79 222 – 227	220 ± 7 79 207 – 230	225 ± 5 85 221 – 229	196
FOL / SVL	509	545 ± 18.31 519 563	548 ± 7 73 543 – 554	524 ± 28 13 465 – 558	547 ± 18 37 534 – 560	554
FTL / SVL	306	330 ± 10 13 315 – 338	332 ± 0 96 331 – 333	313 ± 18 46 273 – 337	336 ± 11 74 328 – 344	324
HAL / SVL	219	190 ± 14 08 173 – 203	203 ± 9 9 196 – 210	201 ± 11 87 180 – 221	208 ± 4 94 204 – 211	221
HL / SVL	380	391 ± 12 67 373 – 402	376 ± 9 9 369 – 383	393 ± 18 07 363 – 416	385 ± 3 82 382 388	329
HW / SVL	344	337 ± 4 11 332 – 342	352 ± 0 44 351 – 352	346 ± 16 27 319 – 367	359 ± 0 87 359 – 360	360
IBE / SVL	208	226 ± 4 59 221 231	214 ± 4 05 212 217	233 ± 12 84 217 251	241 ± 11 24 233 249	246
IFF / SVL	144	141 ± 6 62 135 – 148	139 ± 3.66 137 – 142	153 ± 9 5 141 – 169	167 ± 8 84 161 – 173	142
IMT / SVL	45	50 ± 2 86 47 – 53	51 ± 0 46 51 – 52	52 ± 3 94 47 – 57	53 ± 0 83 52 53	48
IN / SVL	75	72 ± 4 48 68 78	70 ± 1 75 69 – 71	73 ± 4 47 66 – 79	76 ± 0.12 76 – 76	69
ITL / SVL	113	116 ± 5 48 111 – 123	119 ± 5 82 115 – 123	118 ± 6 39 108 – 125	118 ± 5 53 114 – 122	125
IUE / SVL	45	53 ± 5 47 – 59	48 ± 2.32 47 – 50	49 ± 5 7 40 – 58	40 ± 0.17 40 – 40	50
MBE / SVL	151	150 ± 14 25 137 – 169	157 ± 12 44 148 – 166	164 ± 17 68 143 – 193	139 ± 4 75 136 42	140
MFE / SVL	226	254 ± 10 19 240 – 265	244 ± 2 26 242 246	255 ± 17 95 229 – 279	243 ± 5 3 239 247	221
MN / SVL	311	331 ± 10 09 317 – 339	323 ± 2 97 321 325	339 ± 19 96 304 373	333 ± 7 0 3 328 – 338	306
SVL	57 6	42 9 ± 555 36 4 – 49 8	51 1 ± 1 34 50 1 52 0	48 1 ± 6.86 36 2 – 54 2	46 8 ± 2 48 45 0 48 5	444
TFL / SVL	116	123 ± 7 07 114 130	120 ± 5 85 116 124	122 ± 9 53 105 – 135	125 ± 5 12 122 129	130
TL / SVL	500	515 ± 18 78 488 530	528 ± 1 34 527 529	508 ± 20 82 465 – 534	507 ± 2 64 505 509	532
TYD / SVL	63	64 ± 2 09 62 66	62 ± 3 75 60 65	65 ± 2 94 62 71	68 ± 5 56 64 72	66
TYT / SVL	43	39 ± 3 35 35 44	39 ± 2 83 37 41	39 ± 5 77 27 49	41 ± 3 69 39 – 44	35
ULW / SVL	83	86 ± 3 84 81 89	78 ± 1 16 77 – 79	90 ± 3 84 86 – 98	93 6 ± 0 0 93 6	88
WTF / SVL	68	73 ± 8 94 65 – 85	81 ± 1 22 80 – 82	76 ± 12 3 52 86	87 ± 4 63 84 91	102
WT / SVL	65	76 ± 4.88 72 – 82	83 ± 5 76 79 87	78 ± 8 54 63 90	88 ± 6 59 83 – 92	83
WTI / SVL	50	58 ± 11 52 49 75	68 ± 0 89 67 – 69	58 ± 7 84 47 68	68 ± 3 6 65 – 71	79
WTL / SVL	74	85 ± 10 56 77 – 100	94 ± 0 68 93 – 94	88 ± 8 37 76 – 100	98 ± 8 13 92 – 104	98

Source - MNHN, Paris

Un nouveau *Leptopelis* de la zone forestière camerounaise (Amphibia, Anura, Hyperoliidae)

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A new species of *Leptopelis* from southern Cameroon is described. It is readily distinguishable by its dorsal pattern, transversely striped except a trapezium-shaped cephalic blotch, very rounded canthus rostralis, immaculate ventrum and characteristic nuptial call. The distribution of this rare species is traced, mainly from aural records, and information on its etho-ecology including the "phonocenosis" to which it participates is given.

Hormis une analyse de ses appels sous la dénomination de "*Leptopelis* sp. 2" (AMIET & SCHIOTZ, 1974), l'espèce décrite ici n'a jamais été mentionnée dans la littérature batrachologique concernant le Cameroun, et plus généralement l'Afrique centrale (PERRET, 1966; LAURENT, 1973; SCHIOTZ, 1999). Sa découverte illustre bien l'utilité, voire la nécessité, de la prospection acoustique en forêt équatoriale : c'est l'audition de vocalisations non identifiables qui a permis de capturer le premier individu en 1972, et les 14 autres spécimens (sauf l'unique femelle) ont aussi été pris grâce à un repérage acoustique préalable. Contrairement à *Leptopelis omissus* Amiet, 1991, la nouvelle espèce n'a été relevée que dans de rares localités de la zone forestière, et les sites d'activité vocale, étroitement circonscrits, ne regroupent que quelques mâles. Il n'y a donc rien d'étonnant à ce que l'espèce, pourtant facile à reconnaître, soit restée inconnue jusqu'ici.

L'holotype et la moitié des paratypes sont déposés au Muséum national d'Histoire naturelle de Paris (numéros précédés par le sigle MNHN), les autres sont actuellement dans la collection de l'auteur (sigle JLA). Les indications relatives au sexe et à l'origine des spécimens étudiés sont regroupées dans le tableau 1.

Pour alléger le texte, les noms des auteurs et les dates de création des espèces citées sont mentionnés ci-après (ordre alphabétique) : *Afrixalus paradorsalis* Perret, 1960, *Alexteroon obstetricans* (Ahl, 1931), *Ammirana albolabris* (Hallowell, 1856); *Ammirana ammicola* (Perret, 1977), *Astylosternus batesi* (Boulenger, 1900), *Bufo gracilipes* Boulenger, 1900, *Bufo tuberosus* Günther, 1859, *Cardioglossa escalerae* Boulenger, 1903, *Cardioglossa gracilis* Boulenger, 1900, *Cardioglossa gratiosa* Amiet, 1972; *Cardioglossa leucomystax* (Boulenger, 1903), *Chiromantis rufescens* (Günther, 1868), *Conraua crassipes* (Buchholz & Peters, 1875), *Dimorphognathus*

Source : MNHN, Paris

Tableau 1 - *Leptopelis zebra*, références et origine du matériel étudié JLA, numéros de collection de l'auteur; MNHN, numéros des spécimens déposés au Muséum national d'Histoire naturelle de Paris. Sexe: M, mâle; F, femelle. L'holotype est signalé par un astérisque.

JLA	MNHN	Sexe	Localité	Coordonnées	Altitude	Date
72 134		M	Ototomo	11°17' E x 3°40' N	env. 720 m	18.II.72
72 466		M	Ototomo	11°17' E x 3°40' N	env. 720 m	30.VI.72
74 003	2000.2712	M	Ototomo	11°17' E x 3°40' N	env. 720 m	7.I.74
74.005	2000.2713	M	Ototomo	11°17' E x 3°40' N	env. 720 m	14.I.74
74.006		M	Ototomo	11°17' E x 3°40' N	env. 720 m	14.I.74
74.016	2000.2714	M	Awae	11°51' E x 3°53' N	env. 700 m	24.I.74
75.293*	2000.2715*	M	Ototomo	11°17' E x 3°40' N	env. 720 m	23.VI.75
75 297	2000.2716	M	Ototomo	11°17' E x 3°40' N	env. 720 m	8.VII.75
75 298		M	Ototomo	11°17' E x 3°40' N	env. 720 m	8.VII.75
78 176		M	Kala-Afomo	11°22' E x 3°50' N	env. 740 m	10.VII.78
78 177		M	Kala-Afomo	11°22' E x 3°50' N	env. 740 m	10.VII.78
78 178		M	Kala-Afomo	11°22' E x 3°50' N	env. 740 m	10.VII.78
78 179	2000.2717	M	Kala-Afomo	11°22' E x 3°50' N	env. 740 m	10.VII.78
78 180	2000.2718	F	Kala-Afomo	11°22' E x 3°50' N	env. 740 m	10.VII.78
79 001	2000.2719	M	Kala-Afomo	11°22' E x 3°50' N	env. 740 m	12.I.79

africanus (Hallowell, 1857); *Hyperolius endjami* Amiet, 1980, *Hyperolius kuligae* Mertens, 1940; *Hyperolius ocellatus* Gunther, 1859; *Hyperolius platyceps* (Boulenger, 1900); *Leptopelis aubryi* (Duméril, 1856); *Leptopelis boulengeri* (Werner, 1898), *Leptopelis brevirostris* (Werner, 1898); *Leptopelis calcaratus* (Boulenger, 1906), *Leptopelis millsoni* (Boulenger, 1894), *Leptopelis modestus* (Werner, 1898); *Leptopelis notatus* (Buchholz & Peters, 1875); *Leptopelis ocellatus* (Mocquard, 1902), *Leptopelis omissus* Amiet, 1991; *Leptopelis rufus* (Reichenow, 1874), *Opisthothylax immaculatus* (Boulenger, 1903), *Ptychadena aequiplicata* (Werner, 1898).

Leptopelis zebra n. sp.

Matériel étudié

Holotype - Mâle MNHN 2000 2715 (ex JLA 75.293) de la Réserve forestière d'Ototomo, à environ 30 km SSW de Yaoundé, 11°17'E, 3°40'N, 720 m d'altitude, forêt dense de bas fond, 23 VI.75. Mensurations et proportions voir tableaux 2 et 3. Livrée dorsale (en alcool) bien contrastée, avec une douzaine de bandes brunes transverses sur fond beige voir fig. 3.

Source : MNHN, Paris

Tableau 2 Quelques mensurations (en dixièmes de mm) chez *Leptopelis zebra*. L'holotype est signalé par un astérisque. L, longueur du corps, mesurée du bout du museau à l'entrejambe, T, largeur de la tête derrière les yeux; C, longueur de la cuisse, de l'entrejambe au genou, J, longueur de la jambe, de la saillie du genou à celle du talon, P, longueur du pied, du talon à l'extrémité de l'orteil IV; œ, diamètre de l'œil entre les angles palpébraux; ty, plus grand diamètre du tympan; on, distance œil-narine. Valeurs maximales en grasses, valeurs minimales en italiques.

JLA	MNHN	L	C	J	P	T	œ	ty	on
Mâles									
72.134		**375**	**190**	**195**	**270**	**165**	54	**39**	**40**
72.466		330	165	175	235	135	*43*	33	34
74 003	2000 2712	335	180	185	250	150	51	37	35
74.005	2000.2713	350	175	185	235	150	54	33	34
74 006		310	170	170	230	135	50	37	*32*
74.016	2000.2714	*295*	*160*	*165*	*200*	*125*	45	*28*	33
75.293*	2000 2715*	345	195	180	260	160	54	38	39
75.297	2000.2716	360	180	180	240	150	**55**	**39**	**40**
75.298		325	185	180	225	135	49	33	35
78.176		300	165	*165*	220	140	46	33	*32*
78.177		330	170	185	230	150	50	36	36
78.178		360	180	175	240	150	**55**	37	35
78.179	2000.2717	335	170	170	225	150	46	34	37
79.001	2000.2719	350	185	185	250	155	50	38	36
moyenne		335,71	176,43	178,21	236.43	146,43	50,14	35,36	35,57
écart-type		23,19	10,27	8,68	17,59	10,99	3,98	3,13	2,65
Femelle									
78.180	2000.2718	450	245	235	335	190	55	40	43

Paratypes. Treize mâles et une femelle, localités d'origine et dates de capture voir tableau 1.

Autre matériel. – 51 diapositives, 3 enregistrements sonores.

Diagnose. *Leptopelis* sylvicole de taille médiocre, bien caractérisé par (1) son canthus rostralis très arrondi, peu marqué, (2) sa livrée dorsale constituée d'une macule céphalique trapézoïdale et de bandes transverses sur un fond plus clair, (3) sa face ventrale immaculée, de teinte saumon-orange sur le vivant, (4) ses vocalisations. *L. rufus* et *L. millsoni* peuvent avoir

Source : MNHN, Paris

Tableau 3 Quelques rapports morphometriques chez *Leptopelis zebra*. L'holotype est signale par un astérisque. Abreviations: voir la legende du tableau 2. Valeurs maximales en grasses, valeurs minimales en italiques.

JLA	MNHN	C/L	J/L	P/L	T/L	on/œ	ty/œ
Mâles							
72.134		50,67	52	72	44	74,07	72,22
72.466		*50*	53,03	71,21	*40,91*	79,06	**76,74**
74.003	2000.2712	53,73	55,22	74,63	44,78	68,62	72,54
74 005	2000 2713	*50*	52,86	67,14	42,86	74,07	*61,11*
74.006		54,84	54,84	74,19	43,55	*64*	74
74.016	2000.2714	54,24	55,93	67,8	42,37	73,33	62,22
75.293*	2000.2715*	56,52	52,17	**75,36**	46,38	72,22	70,34
75.297	2000.2716	*50*	50	*66,67*	41,67	72,72	70,9
75.298		**56,92**	55,38	69,23	41,54	71,42	67,34
78.176		55	55	73,33	**46,67**	69,56	71,73
78.177		51,52	**56,06**	69,7	45,45	72	72
78.178		*50*	*48,61*	66,67	41,67	79,06	67,27
78.179	2000.2717	50,75	50,75	67,16	44,78	**80,43**	73,91
79 001	2000.2719	52,86	52,86	71,43	44,29	72	76
moyenne		52,65	53,19	70,47	43,64	73,04	70,59
écart-type		16,74	16,80	22,74	14,05	23,82	26,46
Femelle							
78.180	2000 2718	54,44	52,22	74,44	42,22	72,73	22,63

un patron dorsal similaire mais se distinguent aisément de *L. zebra* par leur bande interoculaire etroite et subrectiligne et par la présence d'au moins quelques macules ventrales foncees.

Etymologie – Allusion aux bandes transversales qui ornent le pelage du zèbre (latin *zebra*).

Habitus, proportions, membres, tegument – Les tableaux 2 et 3 donnent les principales mensurations et proportions relatives aux 14 mâles recoltes, adultes puisque vocalement actifs. Avec une longueur museau anus variant de 29,5 à 37,5 mm (moyenne 33,5 mm), ces mâles ont une taille mediocre par rapport à celle des autres especes forestières camerounaises, mais cependant un peu supérieure a celle de *L. omissus* (29,5 à 35,5 mm, moyenne 32 mm) et, surtout, de *L. modestus* (26 à 28,5 mm, moyenne 27 mm). L'habitus peut être qualifié de "moyen", sans disproportions apparentes. La tête est modérément dilatée, sa largeur repré-

Source : MNHN, Paris

sentant de 41 à 46 % environ de la longueur totale, et les membres postérieurs sont relativement courts pour une espèce à mœurs très arboricoles.

Le museau est court, la distance œil-narine représentant environ les trois-quarts du diamètre oculaire (moyenne 73 %); il est fortement déclive à son extrémité qui, vue de dessus, a un aspect tronqué ou en arc très arrondi; les narines, peu saillantes, sont largement écartées, l'espace internasal représentant environ 80 % de l'espace interorbitaire. Un caractère important de l'espèce est l'atténuation des canthus, plus arrondis que chez les autres *Leptopelis* forestiers et passant à des lores faiblement obliques et à peine concaves. Les yeux sont gros et saillants, le diamètre interpalpébral mesurant de 4,3 à 5,5 mm (moyenne 5 mm). Ce diamètre est supérieur à la distance œil-narine (3,2 à 4 mm, moyenne 3,5 mm) et à celui du tympan (2,8 à 3,9 mm, moyenne 3,5 mm). Ce dernier est circulaire, contigu à l'œil et saillant vers le bas, au-dessus de la commissure buccale; il est entouré plus ou moins complètement par un fin rebord granuleux.

La main (fig. 1), du repli cutané du poignet à l'extrémité du doigt III, est un peu plus longue que l'avant-bras (d'un cinquième environ). Les doigts sont relativement courts et larges, impression accentuée par les replis cutanés qui les bordent jusqu'aux disques adhésifs terminaux. Ces derniers sont aussi larges ou un peu plus larges que longs aux doigts II, III et IV, celui du doigt I étant un peu plus long que large, proportions qui se retrouvent chez la plupart des *Leptopelis* arboricoles. Il y a un tubercule sous-articulaire sous les doigts I et II, deux sous les doigts III et IV; ces tubercules sont très saillants, en particulier les tubercules distaux des doigts III et IV, en forme d'épaisses lames bifides, le tubercule proximal du doigt IV est, comme chez d'autres *Leptopelis*, un peu décalé vers le bord externe du doigt. La paume porte de grosses granulations irrégulières, qui s'étendent sur la base des doigts. Entre les doigts I et II, la membrane interdigitale est étroite, guère plus large que la frange cutanée des doigts, elle est plus étendue entre les doigts II et III et, surtout, III et IV, où son bord libre se situe au niveau de la mi-distance entre les tubercules proximaux et distaux de ces derniers, elle porte, sur sa face inférieure, des verrucosités semblables à celles de la paume, mais plus petites.

Des mensurations effectuées à titre comparatif sur des spécimens de *L. omissus*, *L. calcaratus*, *L. modestus* et *L. aubryi* ont montré que le membre postérieur est relativement plus court que chez toutes ces espèces, y compris, mais de peu, la dernière. La jambe est légèrement plus longue que la cuisse, chacune représentant un peu plus de la moitié de la longueur museau-anus (tableau 3). Le pied (fig. 1) ne présente pas de caractère particulier, et ressemble beaucoup à celui de *L. omissus* (AMIET, 1991). Les orteils sont largement rebordés, les disques adhésifs à peu près aussi longs que larges aux orteils II, III et V, celui de l'orteil I est un peu plus long que large et celui de l'orteil IV un peu plus large que long. Les tubercules sous-articulaires sont très saillants, les plus développés de forme conique, et ont la même répartition que chez les autres espèces du genre, un aux orteils I et II, deux aux orteils III et V et trois à l'orteil IV, le tubercule distal de ce dernier est plus ou moins dédoublé, ce caractère étant variable suivant les individus. La palmure pédieuse est assez étendue entre les orteils III et IV et IV et V, sa partie la plus concave arrive au niveau du tubercule sous-articulaire médian de l'orteil IV, elle est plus profondément échancrée entre les orteils I et II et II et III. Le tubercule métatarsien interne est bien développé, à peu près aussi long que l'orteil au-delà du tubercule sous-articulaire, il est bien saillant, assez comprimé mais avec une arête obtuse. Il y a des petites excroissances plantaires, mais elles sont moins prononcées que sous la main.

Source : MNHN, Paris

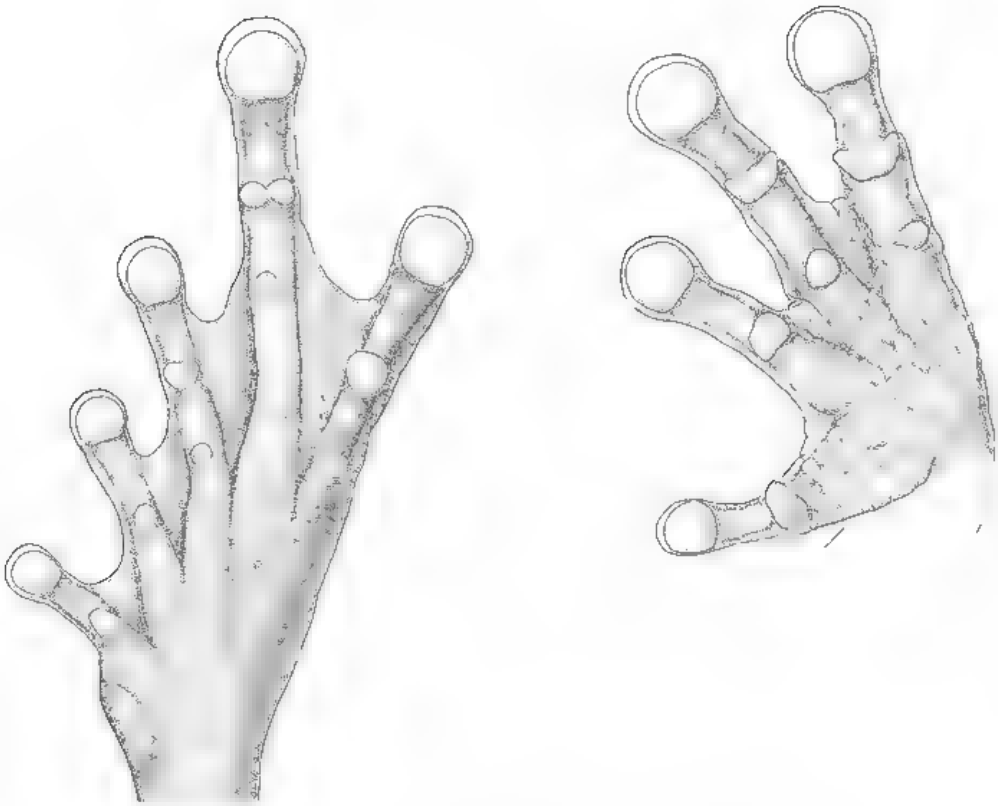


Fig. 1 – Face plantaire du pied et face palmaire de la main chez *Leptopelis zebra*.

Sur le dessus de la tête, du dos et des membres, le tégument est très finement et densement granuleux, ce qui lui donne un aspect mat; sur les flancs, les granulations deviennent plus grosses et plus inégales. Sur la face ventrale, il est opaque, réticulé-granulé, les granulations étant plus grosses dans les régions pectorale et abdominale que dans la région gulaire. Chez les mâles, près de la racine des bras, deux petites plages circulaires de 3 mm de diamètre environ, d'aspect lisse mais en fait finement poreuses, correspondent aux glandes pectorales. Sous les cuisses, la peau est en partie transparente, avec des petits polygones opaques d'aspect pavimenteux. La tranche externe des avant-bras et des pieds est soulignée par un net repli cutané, s'étendant jusqu'à l'extrémité du doigt et de l'orteil externes.

Pigmentation – La teinte de fond de la face dorsale (fig. 2) varie du mastic au beige clair ou au fauve, avec le plus souvent une chaude nuance orangée sans équivalent chez les autres *Leptopelis* camerounais. Le dessin (fig. 3), très caractéristique, est constitué par des bandes transversales brun clair, assez régulières, se succédant depuis le dessus du museau jusqu'à la région lombaire; ces barres sont plus ou moins nombreuses et étroites suivant les individus. Sur la tête, une épaisse barre interoculaire constitue la base d'un trapèze ou d'un triangle à sommet orienté vers l'arrière : il s'agit en fait de la macule céphalique, présente chez de nombreuses autres espèces de *Leptopelis*, mais ici largement évidée dans sa partie centrale

Source : MNHN, Paris

Fig. 2 Mâles de *Leptopelis ebra* (a) Ototomo, 18 II 72, (b) Ototomo, 7 I 74 (JLA 74 005) (c) Kala, 10 VII 78 (JLA 78 176) la coloration rouge des orteils et des doigts n'est visible que chez certains individus, (d) Ototomo, 18 II 72 (JLA 72 134) livrée diurne à dessin imperceptible, (e) Ototomo, 7 I 74 (JLA 74 006): chez cet individu en livrée diurne le dessin est atténué, mais la fine granulation tégumentaire et les points noirs, présents chez certains individus, sont plus apparents, (f) Awae, 24 I 74 (JLA 74 016) malgré la surexposition de la région guulaire, une teinte verte reste visible sur les côtes de la gorge (g) Ototomo, 18 II 72 (72 134) face ventrale, à forte saffusion saumonée, de l'individu figuré en (d)

Source : MNHN, Paris

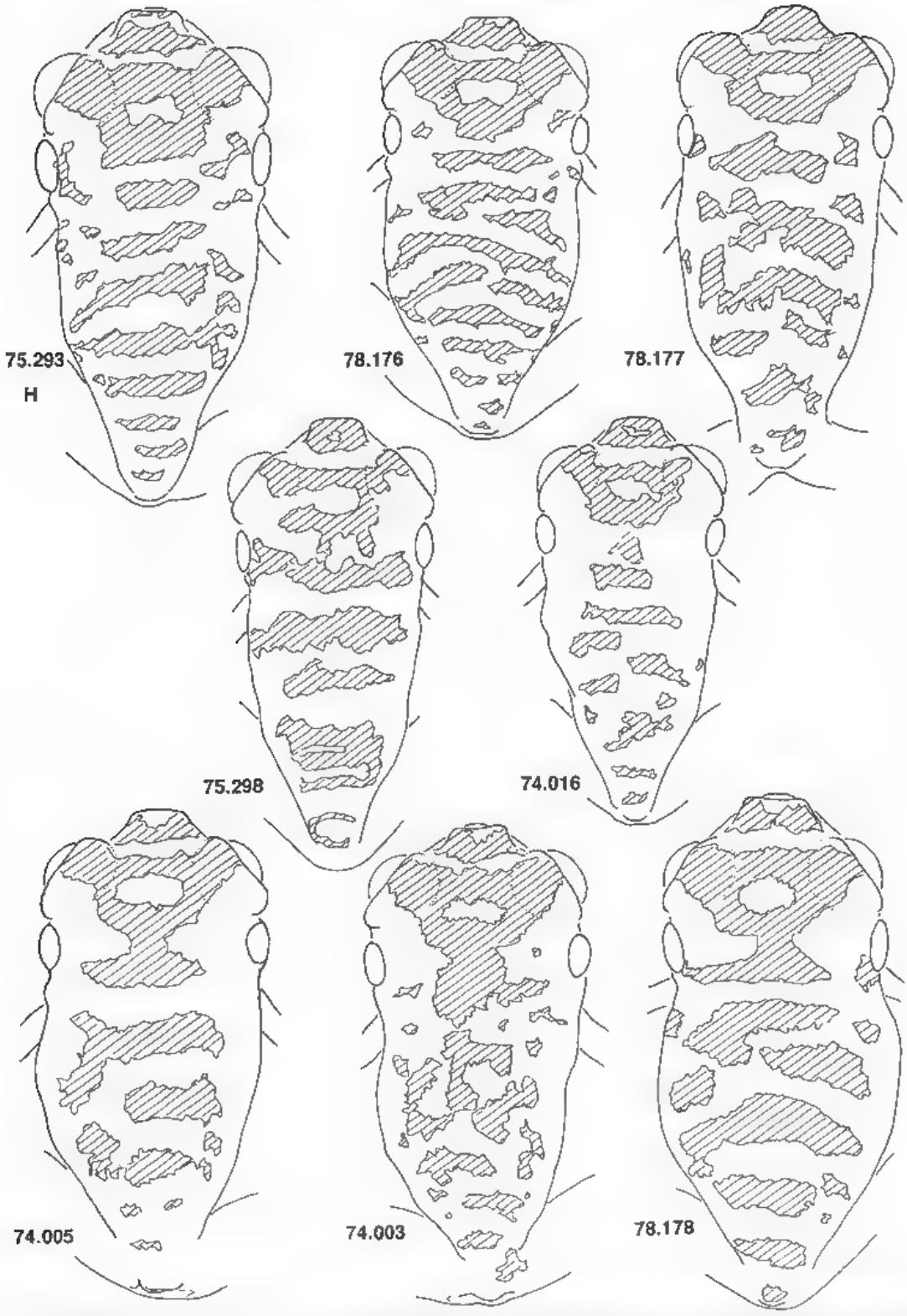


Fig. 3. Variation du patron dorsal de *Leptopelis zebra*, dessins à la chambre claire schématisés. Les numéros sont ceux de la collection de l'auteur (voir tableau 1). H, holotype (JLA 75.293 = MNHN 2000.2715).

Source : MNHN, Paris

Cette ornementation céphalique est un caractère discriminant important par rapport à *L. rufus* et *L. millsoni*, dont le dessin dorsal peut être aussi, assez souvent, formé de bandes transverses. chez ces derniers, il n'y a pas de macule céphalique mais uniquement une bande interoculaire étroite, très régulière et indépendante des autres éléments du patron dorsal De plus, chez *L. rufus* et *L. millsoni*, les fascies dorsales sont souvent réunies par des anastomoses médio-dorsales et circonscrites par un liséré foncé plus apparent que chez *L. zebra*.

Le dessus des avant-bras et des jambes est aussi orné de bandes transversales, dont la densité et la largeur reproduisent celles du dos, avec les mêmes variations individuelles.

Comme chez de nombreuses espèces de *Leptopelis*, il peut y avoir quelques petits points blancs ou, plus souvent, noirs (fig. 2b, e), correspondant à des granulations un peu plus grosses, dispersés sur le dos et le dessus des jambes, mais pas sur la tête. Il n'y a aucune trace de pigmentation verte chez les 15 spécimens étudiés.

L'ornementation latérale est très sobre. Les côtés de la tête ne montrent ni pigmentation sombre sub-canthale, ni macule blanche sous-oculaire, contrairement à de nombreuses autres espèces de *Leptopelis*. Les flancs sont unis, de la même teinte que le dos mais plus clairs, ou tout au plus mouchetés de brun (fig. 2a) La coloration de l'œil n'en est que mieux mise en valeur, l'iris, d'un cuivreux doré, étant surmonté d'une bande d'un rouge sang (fig. 2a-d), beaucoup plus soutenu que chez les autres espèces camerounaises ayant la même pigmentation oculaire (*L. millsoni*, *L. modestus*, *L. omissus* et certains *L. aubryi*) Dans la région postérieure, une macule foncée périanale, surmontée d'un étroit liséré blanc, est reprise au niveau des talons et se poursuit en une bande irrégulière sous le bord externe du tarse: cette ornementation n'a rien de particulier et se retrouve chez presque tous les *Leptopelis* camerounais.

La description précédente concerne des individus à livrée contrastée, se développant sous une forte hygrométrie et une faible luminosité. Dans des conditions inverses, le contraste s'atténue, au point que les bandes dorsales peuvent devenir difficilement perceptibles (fig. 2d-e).

Le dessous des régions gulaire, pectorale et abdominale est remarquable par sa pigmentation unie, sans aucune trace de maculation La gorge est blanche, mais peut présenter une teinte turquoise chez certains individus (fig. 2f), orangée chez d'autres (fig 2g) Ces différences ne paraissent pas individuelles, mais plutôt liées aux conditions ambiantes: mes notes de terrain mentionnent, à plusieurs reprises, que la couleur vert turquoise de la gorge ne se voit que la nuit, pendant le chant, alors que les photos d'individus fortement éclairés au préalable, faites en laboratoire, ne montrent pas cette coloration La poitrine et l'abdomen sont blancs ou lavés d'orangé. Le dessous des mains, des pieds et des cuisses est toujours coloré de saumon, pouvant tirer sur le rouge clair ou l'orange. Le dessous des cuisses est très caractéristique, avec des granulations plates polygonales d'un blanc opaque ressortant sur le reste du tégument, transparent et vivement colore. Le même contraste s'observe pour le pli cutané bordant les membres antérieurs et postérieurs, lui aussi de teinte blanche. Assez paradoxalement, le *dessous* du tarse est, sur son bord externe, fortement pigmenté de brun, coloration qui se poursuit le long du cinquième orteil.

En alcool, toute la face ventrale est blanchâtre, les zones transparentes devenant opaques. Sur la face supérieure, le patron à bandes transversales reste visible, du moins si l'animal a été fixé en livrée contrastée.

Source : MNHN, Paris

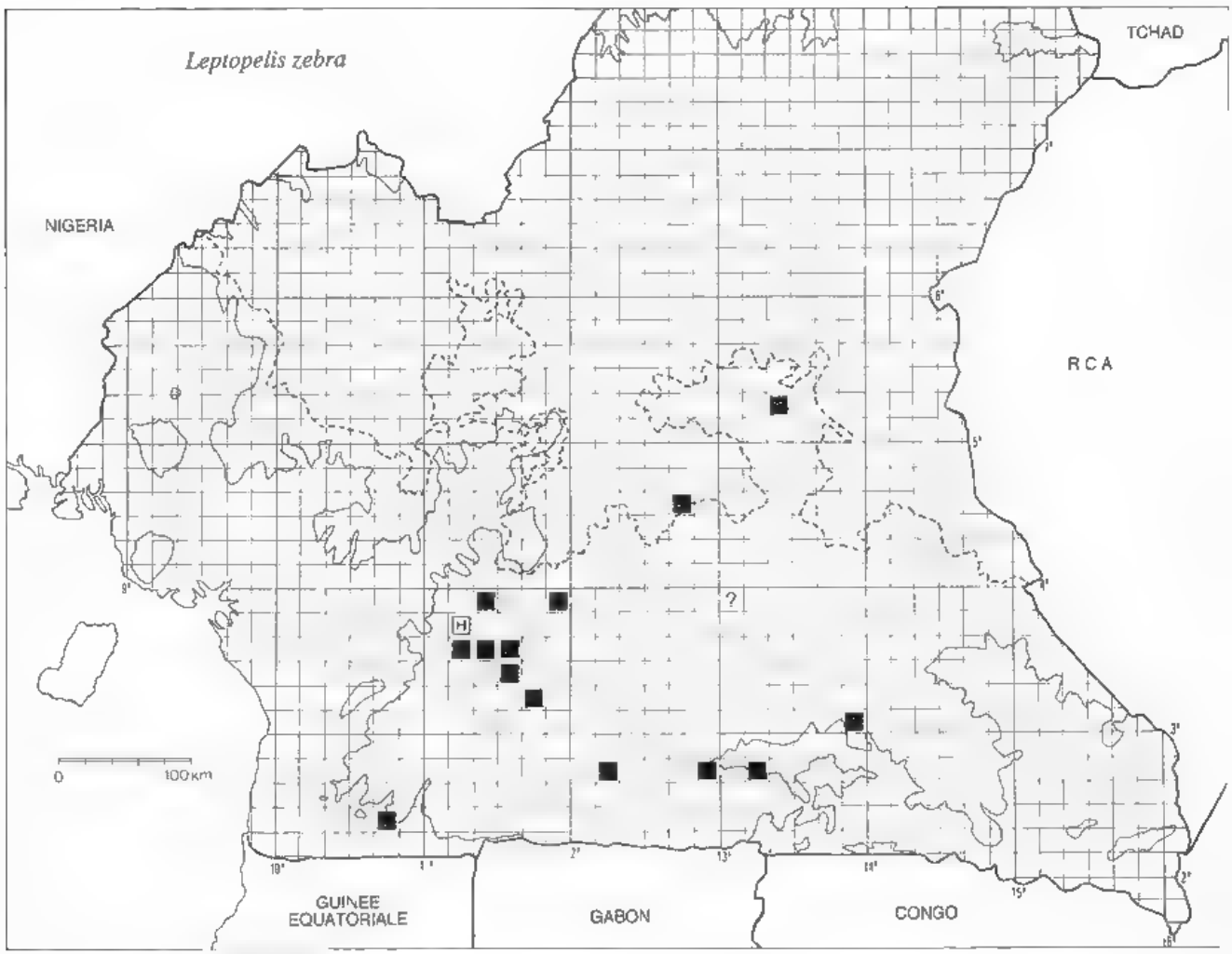


Fig 4 Carte du Cameroun au sud du 8e parallèle montrant les carres (de 10 minutes sexagesimales de côté) où la présence de l'espece a ete relevee. En trait plein courbe de niveau de 600 m, en tirete limite nord de la forêt dense continue.

Distribution geographique Comme le montre la carte de la fig 4, tramee en carres de 10 mn de côté (pour la méthode de cartographie, voir AMIET, 1983), la présence de l'espece a eté relevee dans une quinzaine de carrés seulement, ce qui est tres inférieur aux chiffres atteints par la plupart des autres *Leptopelis* sylvicoles (*L. omissus* 122, *L. calcaratus* 91, *L. brevirostris* 83; *L. boulengeri* 65, *L. millsoni* 54, *L. ocellatus* 51; *L. rufus* 46) L'aire de l'espèce englobe le centre et l'est du Cameroun, avec une limite nord coïncidant apparemment avec celle de la forêt dense et une limite ouest constituee par le rebord du Plateau sud-camerounais. Les prospections dans la plaine littorale et l'ouest du Cameroun ont été assez denses pour qu'on puisse considérer l'absence de *L. zebra* dans ces regions comme etablie En revanche, les grandes lacunes dans l'est et le sud-est du territoire sont probablement dues à un manque de prospections aux periodes favorables. D'autres Anoures camerounais ont une distribution

Source : MNHN, Paris

semblable (par exemple *Hyperolius platyceps*, *Leptopelis ocellatus* et *Cardioglossa escalerae*), paraissant correspondre à un aréotype "congolais" (AMIET, 1983).

Ecologie en période de reproduction. – Les sites où ont été entendus les mâles de *L. zebra* présentaient plusieurs caractéristiques communes: (1) localisation dans des vallées plates, parcourues par de petites rivières forestières à cours lent, sur fond de sable, gravier et feuilles mortes, (2) substrat parsemé, en saison pluvieuse, de trous d'eau ou de flaques, sans être franchement marécageux: au moins en grande saison sèche, ces collections d'eau sont taries, (3) végétation dense, enchevêtrée, où l'abondance des lianes et les discontinuités de la canopée évoquent souvent des formations secondaires âgées.

Les postes de chant, fournis par des branchettes ou des lianes, se situent nettement plus haut que pour les autres *Leptopelis* forestiers, *L. omissus* compris. Leur hauteur, difficile à estimer dans un sous-bois dense, a souvent paru atteindre la dizaine de mètres. Cette situation elevée n'est cependant pas obligatoire, comme l'a montré l'"expérience naturelle" suivante.

Le site de Kala-Afomo, ou quelques mâles appelaient à chaque saison de reproduction a proximité d'une petite mare tapissee de feuilles mortes, a été profondément transformé par un défrichement effectué fin 1977. Les grands arbres ont été abattus, et seuls ont subsisté a proximité de la mare des arbustes, des grandes herbacées et des masses de lianes privées de leurs supports. Les mâles de *L. zebra* se sont alors établis dans cette végétation broussailleuse proche de la mare, émettant leurs appels à seulement 2 ou 3 m du sol, ce qui a permis d'en capturer plusieurs, auxquels s'est ajoutée la seule femelle connue de l'espèce. La croissance de la végétation, rapide dans ce type de milieu, a entraîné, au fil des saisons, une remontée des postes de chant.

Vocalisations. Cycle annuel d'activité vocale. – Les appels se distinguent facilement de ceux des autres *Leptopelis* camerounais. Ils consistent en 3 ou 4 notes, d'une durée de 0,2 s et séparées par des intervalles d'environ 1 s, qui pourraient être transcrites par des "hon" assez graves; la dernière note est plus sonore que les precédentes. Ce type d'appel est le plus souvent émis mais, sporadiquement, il peut y avoir des notes plus courtes, "konk" à tonalité nasale et grave. Un sonagramme a été publié sous la dénomination "*Leptopelis* sp. 2" (AMIET & SCHIOTZ, 1974) mais il est en partie obscurci par une épaisse bande de bruit de fond. Il permet cependant de constater le faible niveau de la fréquence dominante.

Trois localités de la région de Yaounde ont permis de suivre le cycle d'activité vocale de l'espèce: Ototomo (janvier 1972 a décembre 1975), Kala-Afomo (janvier 1973 à décembre 1984) et Nkoladjap-Ekombitie (janvier 1976 à décembre 1984). Le tableau 4 donne le détail des relevés acoustiques mensuels effectues dans ces localités, ainsi que le nombre de releves au cours desquels l'espèce a été entendue (il n'y a pas eu de sorties en août et pendant la première quinzaine de septembre).

Ce tableau permet de constater qu'il y a deux périodes d'activite vocale, separees par des phases durant lesquelles l'espèce est totalement silencieuse. L'une va de decembre à mars et l'autre comprend au moins juin et juillet. Il faut toutefois preciser qu'une analyse plus fine des dates des releves montre que l'espece a été notee une seule fois avant la mi-decembre et jamais au-delà du 7 mars, ce qui ramène à une période d'activité d'un peu moins de trois mois. De même, l'espece n'a été entendue qu'une seule fois (tres peu active) un 12 juin, les autres releves

Source : MNHN, Paris

Tableau 4. Activité vocale de *Leptopelis zebra* dans trois localités de la région de Yaoundé. NR, nombre de relevés acoustiques effectués (les tirets correspondent à des mois où aucun relevé n'a été effectué), RZ, relevés au cours desquels *L. zebra* a été entendu.

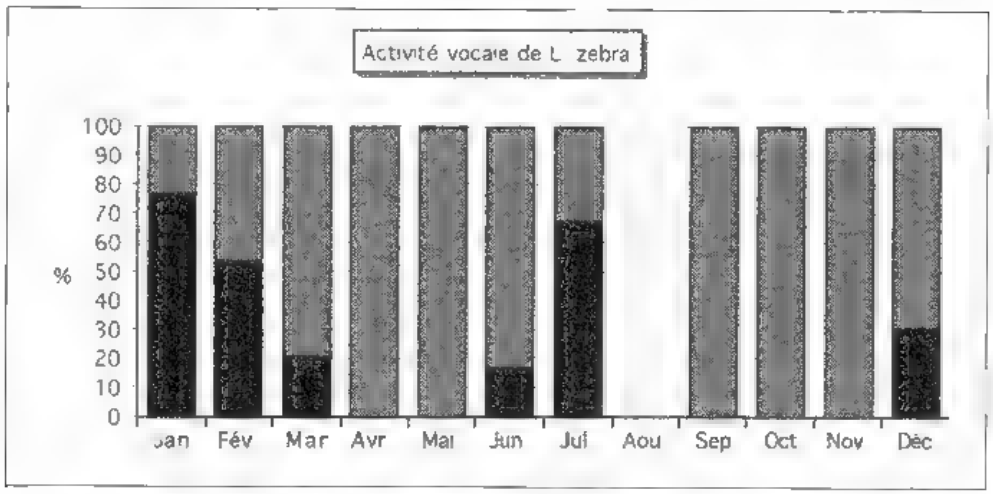
		Jan	Fév	Mar	Avr	Mai	Jun	Jul	Aou	Sep	Oct	Nov	Déc
Ototomo	NR	5	6	4	4	4	3	4	-	-	-	4	4
	RZ	4	6	3			2	4	-	-	-		1
Kala-Afomo	NR	12	11	11	12	12	12	13	-	13	13	13	13
	RZ	11	4				2	8	-				4
Nkoladjap / Ekombitié	NR	9	9	9	9	8	8	8	-	10	9	9	9
	RZ	5	3	2				5	-				3
Total	NR	**26**	**26**	**24**	**25**	**24**	**23**	**25**	-	**23**	**22**	**26**	**26**
	RZ	**20**	**13**	**5**			**4**	**17**	-				**8**

du même mois se situant après le 20, la lacune de prospection en août ne permet pas de savoir quand s'achève cette seconde période, mais il est probable que les dernières émissions sonores ont lieu début septembre. Les autres relevés effectués dans des localités proches de Yaoundé coïncident aussi avec ces deux périodes. En revanche, plus à l'est, dans le domaine de la forêt mésophile ou de la forêt congolaise, il semble y avoir un décalage des périodes d'activité car l'espèce a été entendue fin mars à Mintom (13°17'E) et à Mayang (13°56'E) et jusqu'aux 5-6 avril à Sandja (12°47'E).

Comme le montrent les graphiques de la figure 5, il y a une étroite corrélation entre les périodes d'activité vocale et les deux saisons sèches caractéristiques des climats équatoriaux. Il faut cependant remarquer que: (1) la petite saison sèche (juillet-août) ne s'accompagne pas d'une baisse marquée de l'hygrométrie et peut même, certaines années, être quasi virtuelle, (2) le commencement de la grande saison sèche peut varier, dans la région concernée, du début à la fin du mois de novembre. Or ces variations ne se répercutent pas sur les phases d'activité vocale de *L. zebra*, ce qui laisse supposer que celle-ci n'est pas induite par les conditions propres aux saisons sèches.

Plusieurs autres espèces forestières, surtout des *Leptopelis* et des *Cardioglossa* (AMIET, 1989), ont un cycle semblable, mais celui de *L. zebra* est remarquable par le fort "resserrement" des périodes d'activité vocale. Ce phénomène est probablement en relation avec les faibles effectifs des mâles actifs dans un site donné: les relevés acoustiques ont souvent reposé sur l'audition de 3 ou 4 mâles seulement, alors que, simultanément, les autres espèces de *Leptopelis*, *L. omissus* en particulier, étaient représentées par des dizaines de mâles actifs. A l'extrême, certaines saisons de reproduction ont donné l'impression d'être "sautées", aucun mâle n'ayant été entendu dans un site et à une date propices. C'est ce qui explique que dans le tableau 4, même lors des meilleurs mois, les relevés positifs ne représentent pas la totalité des relevés effectués.

Source : MNHN, Paris



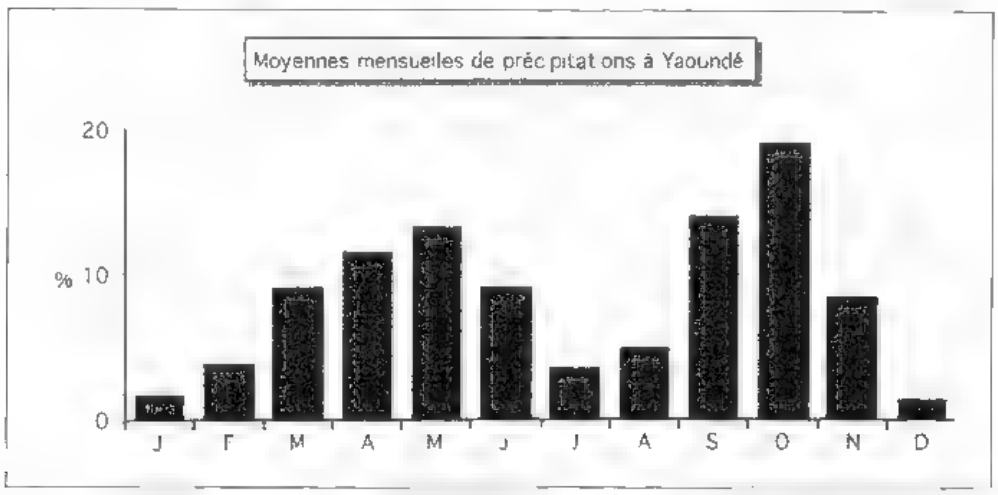


Fig. 5. — Cycle d'activité vocale de *Leptopelis zebra* dans trois localités de la région de Yaoundé (explications dans le texte), comparé au cycle annuel des précipitations. Les données pluviométriques, exprimées en pourcentage du total annuel moyen pour une période de 30 ans (1597 mm), sont empruntées à SUCHEL (1972).

Espèces compagnes de L. zebra *en période d'activité vocale.* — Le tableau 5 regroupe toutes les espèces d'Anoures entendues lors de 61 relevés auditifs durant lesquels l'activité vocale de *L. zebra* a été constatée. Pour chacune des localités suivies (les mêmes que ci-dessus), les relevés de grande et de petite saison sèche ont été distingués. Les relevés effectués à Ototomo en 1972 n'ont pas été retenus car, à l'époque, toutes les espèces ne pouvaient être identifiées auditivement. Le rapport du nombre de relevés où une espèce a été entendue au nombre de relevés où l'activité de *L. zebra* a été notée a été exprimé en pourcentage, pour faciliter les comparaisons.

Source : MNHN, Paris

Tableau 5 Anoures participant à la même phonocénose que *Leptopelis zebra*. Explications dans le texte. NT, nombre total de relevés où une espèce a été entendue. Groupes: A, développement en eau stagnante; B, développement en eau stagnante renouvelée (proximité d'un cours d'eau), C, développement en eau courante.

	Ototomo Gde. S. s. (8)	Ototomo Pet. S. s. (5)	Kala Af. Gde. S. s. (19)	Kala Af. Pet. S. s. (11)	Nkol./Ek. Gde. S. s. (13)	Nkol./Ek. Pet. S. s. (5)	NT
Poste de chant sur la végétation							
Groupe A							
Le. omissus	62,5	80	94,7	100	100	100	55
Le. calcaratus	75	80	73,7	91	69,2	80	47
Le. boulengeri	62,5	60	63,1	54,4	53,8	60	36
Le. notatus	25	40	42,1	36,4	100	100	34
Hy. ocellatus	50	60	73,7	72,7	30,7	20	34
Le. ocellatus			89,5	72,7	7,7	-	27
Le. aubryi	62,5	100	5,2	18,2	23	20	17
Af. paradorsalis			10,5	81,9			11
Hy. platyceps	12,5	-			30,7	40	7
Hy. endjami			-	36,4			4
Ch. rufescens	12,5	40	5,2	-			4
Le. modestus			10,5	9,1			3
Hy. kuligae					15,4	-	2
Groupe B							
Le. rufus	37,5	-	68,4	36,4			20
Le. millsoni					61,5	60	11
Groupe C							
Op. immaculatus	62,5	60	84,2	100	46	80	45
Al. obstetricans	50	60			7,7	-	8
Poste de chant au sol							
Groupe A							
Am. albolabris	-	40	15,8	-	38,5	60	13
Pt. aequiplicata	37,5	20					4
Groupe B							
Di. africanus	25	80	100	91	15,4	40	39
Am. amnicola			31,6	9,1	7,7	-	8
Groupe C							
Ca. gratiosa	50	80	79	100	100	100	52
Ca. escalerae	100	80	84,2	82			37
Co. crassipes	37,5	40	63,1	54,5	23	20	27
Ca. gracilis	37,5	60	15,8	100	23	80	27
As. batesi	12,5	20	58	63,6	23	20	24
Ca. leucomystax	75	100	31,6	54,5			23
Bu. gracilipes	25	-	36,8	36,4			13
Bu. tuberosus			36,8	-	15,4		9

Source : MNHN, Paris

On constate que près d'une dizaine d'espèces accompagnent fidèlement *L. zebra*, quelles que soient la localité et la saison considérées, puisqu'elles se retrouvent dans plus de 50 % des relevés: *Leptopelis omissus* (55 relevés sur 61), *Cardioglossa gratiosa* (52), *Leptopelis calcaratus* (47), *Opisthothylax immaculatus* (45), *Dimorphognathus africanus* (39), *Cardioglossa escalerae* (37), *Leptopelis boulengeri* (36), *L. notatus* (34) et *Hyperolius ocellatus* (34).

D'autres especes sont plus souvent notées en même temps que *L. zebra* lors d'une des deux saisons sèches. Par exemple, *Cardioglossa gracilis* est plus fréquente en petite saison sèche. En effet, l'activité vocale de cette espèce, plus "opportuniste" que les autres *Cardioglossa* sylvicoles, débute aux premières pluies de fin février et connaît seulement un ralentissement en petite saison sèche, en relation peut-être avec le maintien d'un degré hygrométrique plus élevé qu'en grande saison sèche.

On remarquera aussi que certaines especes n'accompagnent *L. zebra* que dans certaines localités, probablement en raison de particularités environnementales présentées par ces dernières. C'est ainsi que les bas-fonds de Nkoladjap-Ekombitié, parcourus par de petites rivières à cours lent, sur fond finement sableux, susceptibles de tarir en grande saison sèche (et même en petite), conviennent à *Leptopelis millsoni*, mais pas à *Cardioglossa escalerae* (qui recherche pourtant, en période de reproduction, des substrats sableux).

On pourrait qualifier de "phonocénoses" les ensembles d'espèces qui exercent leur activité vocale, et donc reproductrice, pendant la même période de l'annee et dans des sites présentant des caractéristiques écologiques similaires. Ces ensembles ne sont, à proprement parler, ni des peuplements, ni des communautés, ni des associations, ni des synusies. Ils meritent néanmoins d'être décrits car ils constituent de bons indicateurs de certaines combinaisons de facteurs écologiques, en ayant de plus le grand avantage d'intégrer la dimension temporelle. Dans le cas présent, il faut cependant remarquer que le tableau 5 ne donne qu'une image incomplète de la phonocénose à laquelle participe *L. zebra*, car il ne tient pas compte (1) des relevés effectués dans les mêmes sites et aux mêmes saisons mais où *L. zebra* n'a pas été noté, (2) des relevés effectues dans les mêmes sites mais à d'autres saisons (ils permettraient de mettre en évidence l'évolution de la phonocénose au cours de l'annee), (3) des relevés effectués dans d'autres milieux (qui permettraient de définir les phonocénoses de façon comparative, en mettant en évidence des espèces "caractéristiques" et/ou constantes). Tel quel, le tableau 5 représente cependant une esquisse significative de la phonocénose a laquelle participe *L. zebra*.

RÉSUMÉ

Une nouvelle espèce de *Leptopelis* provenant du Cameroun méridional est decrite. Elle est facilement reconnaissable par son patron dorsal, constitue de bandes transverses sauf une macule céphalique trapézoïdale, son canthus très arrondi, sa face ventrale depourvue de maculation et son appel nuptial caractéristique. Les limites de repartition de cette rare espèce sont definies, surtout a partir de relevés auditifs, et des informations sont fournies sur son étho-écologie, y compris la "phonocénose" à laquelle elle participe.

Source : MNHN, Paris

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Local variation in *Rana temporaria* egg and clutch size: adaptations to pond drying?

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Egg and clutch size variation among populations of common frogs (*Rana temporaria*) were studied in 14 ponds in Sweden. Also two secondary indices, clutch mass and allocation tactics (egg size^3/clutch size) were studied. For all four characters there was a pond-wise correlation between the values across the two study years. All characters differed among ponds and all but allocation tactics differed between years. At least part of this variation must be environmental. The ponds were classified as permanent or temporary. The latter dried completely in some years, killing all tadpoles. Pond type affected all characters except egg size. Thus, clutches in shallow ponds were smaller, lighter and, correcting for clutch mass, had larger eggs (from the allocation tactics index). I suggest that this variation may be adaptive.

INTRODUCTION

Local character variation is a trait of all non-endemic animal populations. In common frogs (*Rana temporaria*), JOLY (1991) and RYSER (1996) found differences in body size among local populations. My study is concerned with two other life history characters that are well covered by frog studies, namely clutch and egg size (GIBBONS & MCCARTHY, 1986; BERVEN, 1988; TEJEDO, 1992; SEMLITSCH & SCHMILDHAUSEN, 1994). However most studies are concerned with within-population variation and how this is related to individual strategies (exceptions being JOLY, 1991, and MARTIN & MIAUD, 1999). This is also the approach taken in a number of theoretical studies and reviews of life history theory (SMITH & FRETWELL, 1974, ROFF, 1992, EBERT, 1993). The models can be used to compare optimal trait expression in different localities (CUNNINGTON & BROOKS, 2000).

The question posed in the present study is does population variation in egg and clutch size characters exist in the study area and is this related to pond hydroperiod? Pond hydroperiod is studied because it has a profound effect on the survival of common frog tadpoles in the study ponds (LOMAN, 1996) as well as in other areas (COOKE, 1985, KUTENKOV & PANARIN, 1995). So, in temporary ponds fast developing tadpoles are at an obvious advantage. For some frogs (*Bombina orientalis* PARICHY & KAPLAN, 1995, *Rana sylvatica* BERVEN & CHADRA,

Source : MNHN, Paris

1988), it has been shown that large eggs hatch into fast developing tadpoles. The same correlation has already been found for *Rana temporaria* in the present study area (unpubl.). This makes it particularly interesting to study if there is a relation between pond hydroperiod and egg size, one of the response variables studied here.

One reason local character variation is important to study is this. Basically, the variation may be genetic and/or due to direct environmental effects. If the variation has a genetic basis and is adaptive, this is a factor that must be taken into consideration in conservation work Translocating individuals in order to increase diminishing populations may lead to "ecological outbreeding depression" (SCHIERUP & CHRISTIANSEN, 1996; LARDNER, 2000). This is the case if the introduced genotype is not adapted to the new environment.

METHODS

The study is based on measurements on eggs and spawn clumps collected in the field and on field measurements of the length of the source pond hydroperiod.

During the breeding seasons of 1993 and 1994, spawn clumps were sampled in 14 ponds. All ponds were sampled in both years. The ponds are located in the central and southwestern part of Skåne, the southernmost province of Sweden. The southwesternmost ponds are in the vicinity of Lund, 40 km from the northeasternmost The study ponds were classified as permanent or temporary. Temporary ponds were those eight that in some years dried out before or during the time the tadpoles metamorphosed During the six years 1992-1997, when the ponds were monitored during the time of metamorphosis, this happened 2, 2, 2, 2, 5, 5, 5 and 6 times. The six permanent ponds always contained enough water for the entire period of tadpole life and metamorphosis. The number of spawn clumps laid in the ponds (average of 1993 and 1994) was between 19 and 310 in the temporary and between 16 and 160 in the permanent ponds.

From each pond I collected data on 6 to 22 spawn clumps. Each spawn clump was weighed and a sample of approximately 10 g was collected. The clump was then immediately returned to the pond. The sample was weighed at the pond and brought to the laboratory where the number of eggs in the sample was counted This information was used to estimate "clutch size" (total number of eggs in the clump) The egg diameter (egg proper, excluding jelly) was measured with calipers in a sample of 15 eggs from each clump and the mean value was used as measure of "egg size". Because the ponds were visited every 5 days, I could age the spawn. Only spawn aged one to four days was used

Two secondary indices were computed Clutch volume was computed as the average egg volume times clutch size "Allocation tactics index" was computed as average egg diameter^3 divided by clutch size. A large value of tactics means that a female, relative to other females that make the same total investment (same clutch mass), is more inclined to put her effort in large eggs but a smaller clutch

Source : MNHN, Paris

Table 1 Pearson correlation test between 1993 and 1994 values for the four indexes studied Measurements are defined in the methods section All tests are based on 14 ponds The *P* values are one-tailed probabilities. A one-tailed test was used as any, hypothetical, negative correlations a priori would have been discarded as non sensical

Index	*r*	*P*
Egg size	0 488	0 038
Clutch size	0 820	< 0 001
Clutch mass index	0 870	< 0 001
Allocation tactics index	0 580	0 015

Table 2 – Average clutch and pond values for permanent and temporary ponds. Egg size is diameter (mm), clutch size is number of eggs per clutch and clutch volume is total volume of eggs (cc) Allocation tactics is an index that is explained in the methods *x*, mean, *s*, standard deviation, *n*, sample size

Pond type		Egg size	Clutch size	Clutch volume	Allocation tactics
Permanent	*x*	1 88	1929	6 96	0 0040
	s	*0.12*	*347*	*1.30*	*0.0010*
	n	*6*	*6*	*6*	*6*
Temporary	*x*	1 87	1464	5.26	0 0052
	s	*0 066*	*289*	*1 51*	*0.0009*
	n	*8*	*8*	*8*	*8*

RESULTS

For all four characters (egg size, clutch size, clutch mass index and allocation tactics index), there was a significant correlation between the average value for a pond in 1993 and that in 1994 (tab. 1, fig. 1)

I also tested the independent effects of year, pond and pond type (permanent or temporary) on the four characters. Egg size was larger in 1994 than in 1993. It differed significantly among ponds but there was no effect of pond type (tab. 2-3, fig 1) Clutch size was significantly larger in 1994 than in 1993 and it differed significantly among ponds. Clutches that were deposited in permanent ponds were larger than those in temporary ones (tab 2 3, fig 1) Clutch mass index showed the same pattern as clutch size; higher mass in 1994, a significant effect of pond and on average a higher mass for clutches in permanent ponds (tab 2-3, fig 1) The allocation tactics index differed significantly among ponds but not

Source : MNHN, Paris

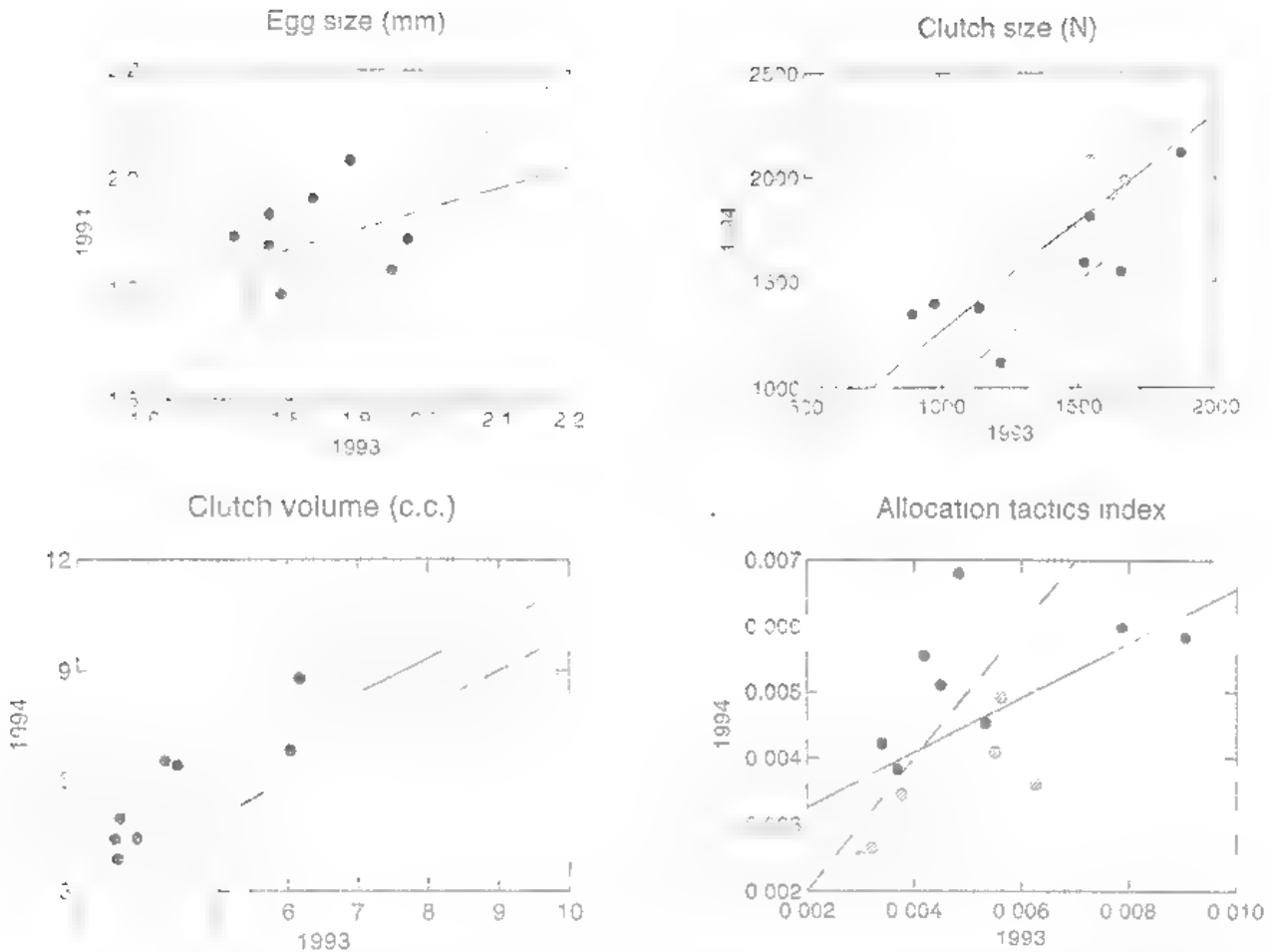

Fig 1. Relation between egg and clutch characters in 1993 and 1994. Permanent ponds are indicated with open circles and temporary ones with filled circles. The dashed line represents equal 1993 and 1994 values. A positive slope of the fitted linear regression (the unbroken line) indicates constancy in pond characteristics over years.

Source MNHN, Paris

Table 3 · Effects from pond (individual pond, nested under pond hydroperiod), pond type (hydroperiod permanent or temporary) and year on egg and clutch characters, tested with a 3-way ANOVA The interaction Pond*Year was tested but not found significant and removed for the definite test. Data are individual clutch measurements

		Egg size	Clutch size	Clutch volume	Allocation tactics
Pond	*df*	11,222	11 224	11·221	11 221
	F	10 23	6 73	7 93	6 59
	P	< 0.001	< 0.001	< 0.001	< 0 001
Type	*df*	1 222	1 224	1 221	1 221
	F	0 015	43 0	22.7	28 3
	P	0 90	< 0.001	< 0.001	< 0 001
Year	*df*	1.222	1 224	1 221	1.221
	F	6.86	16 22	22 0	1 46
	P	0.009	< 0.001	< 0.001	0 23

years. The value was higher for temporary ponds than for permanent ones (tab. 2-3, fig. 1) This means that when correcting for the fact that females breeding in temporary ponds put less effort (a lower clutch mass index) altogether into breeding, they were more inclined to invest in larger eggs.

DISCUSSION

Indeed, there were differences in the four egg and clutch characters studied among populations breeding in different ponds. In previous studies, MARTIN & MIAUD (1999) and JOLY (1991) have detected differences in female size among neighbouring populations. In the Joly study, there were also differences in egg and clutch size between two populations. Because these variables have been shown to be correlated to female size within populations (HONIG, 1966, GIBBONS & MCCARTHY, 1986, JOLY, 1991; RYSER, 1996), it may well be that egg size variation between populations, both in the Joly study and in the present one, is a direct effect of among-population variation in female size In the MARTIN & MIAUD (1998) study, the variation in egg size among populations was weak, despite among-population differences in female size.

Egg size, clutch size and clutch mass index varied between the two years. This was especially clear for clutch size, in all ponds but two were 1994 clutches larger than 1993 clutches. Also for egg size was the average pond value larger in 1994 This pond wide year effect suggests that weather factors are involved but, with only two years available for analysis, it is not possible to analyze which factors are crucial Because the eggs are gradually formed during the preceding summer, there are numerous possibilities. Rainfall and temperature

Source : MNHN, Paris

during any combination of months up to a year before spawning may potentially be involved. Again, because female size affects the clutch and egg size variables, between-year variation in female size may partly be the proximate cause, as suggested by BERVEN (1988) in a study of *Rana sylvatica*. Whatever the exact cues, this shows an environmental effect on egg and clutch size, either directly or indirectly through effects on female size.

Although there was a between-year variation, there was a significant year to year correlation among ponds (tab. 1); some ponds had consistently small eggs and clutches. This stresses the pond specificity. This was also manifest as a significant pond effect (tab. 3) on all variables. The pond effect was partly an effect of pond hydroperiod but note that it was still present when accounting for all effects of hydroperiod (as both factors were included in the ANOVA). These effects may be directly or indirectly (through effects on female size) due to variation in the environment and feeding conditions surrounding the ponds.

Genetic differences have been detected in allozyme studies between close populations of frogs (*Rana temporaria*, REH & SEITZ, 1990, REGNAUT, 1997; LARDNER, 2000, *Bufo calamita*: SINSCH, 1992). Also, frog species with a biology similar to that of *Rana temporaria* have been shown to exhibit natal pond fidelity, this includes *Bufo bufo* (HEUSSER, 1966, READING et al., 1991) and *Rana sylvatica* (BERVEN & GRUDZIEN, 1990). In a study of *Rana sylvatica*, BERVEN (1988) has shown that population differences in clutch hand egg size may have a genetic basis. Is it possible that the variation found in this study is due to microevolution? The design does not allow any definite conclusions. However, if microevolution is involved, one would expect the observed variation to be adaptive.

Was the effect of pond hydroperiod on the clutch mass index, parental investment, adaptive? Yes, possibly. The investment was less in shallow ponds. This means less stress on the female and possibly a higher survival with a better possibility to breed more times (MADSEN & SHINE, 2000). In shallow ponds, where breeding fails completely in some dry years, this means a higher likelihood of at least some surviving offspring during a life-time. Actually, life history theory predicts that iteroparous tendencies should be favoured in unpredictable environments (ROFF, 1992).

It is also possible to find an adaptive effect of the variation in the allocation tactics. Given a fixed total investment (clutch mass), it is reasonable that it is more important to invest in large eggs (hatching into fast developing tadpoles) in temporary than in permanent ponds. Large eggs may hatch into tadpoles that develop faster than those hatched from small eggs (BERVEN & CHADRA, 1988, PARICHY & KAPLAN, 1992), thus decreasing the risk of total loss of recruits in a dry summer when the pond may dry early.

It is surprising that there was no effect of pond hydroperiod directly on egg size (tab. 3). This effect could also be predicted for the same reasons I use above to argue an adaptive explanation for variation in allocation tactics index. However, egg size may (regardless of pond hydroperiod) be affected by female size (HONIG, 1966, GIBBONS & MCCARTHY, 1986, RYSER, 1996). For this variable I have no data for the present ponds and thus I cannot control for it. If female size is not related to pond hydroperiod, such a correlation may mask possible effects of pond hydroperiod on egg size. However, the use of allocation tactics index is a method to control for variation in clutch mass, which means it may in turn control for some of the variation in female size (and other female characters that affect total clutch investment).

Source : MNHN, Paris

If the patterns recorded are indeed adaptive, it is easier to see this as an outcome of a direct, selected genetic effect than as a reaction norm (STEARNS & KOELLA, 1986; SCHLICHTING & PIGLIUCCI, 1998) or phenotypic plasticity. This means that females in all study populations may share the same genotype but this codes for different egg and clutch size strategies under the actual conditions present in the different ponds. This would lead to transgenerational phenotypic plasticity (MOUSSEAU & FOX, 1998). However, eggs are formed during the summer preceding breeding (JØRGENSEN, 1981), far ahead of the females' arrival to the breeding pond. Although complicated pathways based on breeding site fidelity are possible, such explanations seem far fetched.

To sum up, the variation recorded must at least in part be due to environmental effects. The fact that some of the variation was adaptive in ways predicted by life history theory suggests that microevolution was also involved. No direct proof for this is however available. Further studies to reveal the nature of between-pond variation in these characters need to use frogs originating in different ponds and raised in a "common garden" (FAUTH, 1998) from egg to maturity. Comparing the traits of their spawn should provide the necessary evidence.

If local adaptions are indeed involved, this also means that translocating frogs affects the genetic make-up of local target populations. In principle, this could have adverse effects (STORFER, 1999). However, the fact that evolution may have occurred in response to such a "fine grained" habitat variable as pond hydroperiod also means that this evolution may proceed quite quickly. Thus the progeny of translocated individuals are likely to adapt quickly, provided a sufficient genetical basis is provided (LARDNER, 2000).

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